STUDIES IN THE ECOLOGICAL EVOLUTION OF THE ANGIOSPERMS

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PREFACE

In the following pages an attempt is made to deal with an aspect of botanical science which appears to be full of interesting possibilities. The long continued labours of the systematists have led to the accumulation of an enormous mass of literature, mostly descriptive of floral structure and floristic relationships. During recent years, on the other hand, the science of Ecology has made considerable progress in the study of plant behaviour in the field; and in dealing with the vegetative forms of plants, both from the physiological and the morphological standpoints, the advantages of bringing different aspects of botanical analysis more closely into union has already been demonstrated in various directions, as, for instance, in the study of physiological anatomy and experimental morphology. In general, botanists have wisely set their faces, as far as possible, against the tendency to break up their science into distinct and separate branches.

The subject of ecological evolution is distinctly synthetic, in so far as it draws on all the more important branches of botany. Synthesis is always more difficult than analysis and is correspondingly less frequently successful; and I am well aware that many of the theories here outlined may require subsequent modification. I may be allowed, however, to point out that this work is not based entirely on preconceived theories. The study of fossil botany supplies facts, not theories, though it may be admitted that the facts are not so numerous, nor always so well established, as we could wish. In Chapters II and III the phylogeny of the various families of Angiosperms is examined, though the opinions regarding their evolutionary history are, for the most part, not mine but those of the numerous different specialists who have dealt with them in the most recent systematic works. The new conclusions are drawn by correlating these more or less accepted ideas regarding the phylogeny with the geographical distribution of the families. The vegetation of moist-tropical regions, except in so far as it has become differentiated as a result of the influence of the organic

environment, especially competition for space, is older than that of the drier subtropical regions on the one hand, and that of temperate regions on the other.

The last three chapters, which deal in outline with a phylogenetic system of classifying plant forms, contain conclusions which seem to me to follow. None of the ecologists who have devised schemes for classifying plant forms, have so far claimed that their systems had any phylogenetic value, though as a matter of fact, the well-known system of Raunkiaer came very near the one here adopted. This is because Raunkiaer based his scheme on the response to the resting season, which has been, undoubtedly, a most important factor in bringing about differentiation in the forms of plants.

The manner in which the subject was first of all approached through a fairly long-continued study of the tropical, subtropical, and temperate floras of South Africa is sufficiently explained in the text.

I feel rather certain that it is only by approaching a subject of this kind from the tropical end that one can maintain a proper perspective. To view the vegetation of the world with the plants of the north temperate regions always in the foreground produces an effect which is somewhat similar to that obtained by looking at an object through the wrong end of a telescope. Of course I make no claims of merit for the fortunate circumstance that during the past fifteen years I have been placed in a region which is almost ideally suited for this kind of study, but I hope I am duly grateful for the fact.

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CHAPTER I

THE FOSSIL RECORD AND ITS INTERPRETATION

Introduction

Botanists are accustomed to regard the fossil Angiosperm record as somewhat disappointing. In spite of continued hopes—recently further stimulated through the description by Hamshaw Thomas (1925) of angiospermous fruits from the Jurassic—that the fossil record might clear up the difficult question of the origin of the group, it must be confessed that, as yet, no very clear light has been thrown on that subject. In the Lower Cretaceous the Angiosperms are already highly differentiated, so that their beginnings must have been much earlier. We are still quite unable to decide whether the most primitive Angiosperms were closely related to the Mesozoic Cycadeoids (in which case, as Scott has recently pointed out (1924), they are to be connected with the more ancient Williamsonian tribe rather than with the Bennettiteae), or whether they are to be connected with other gymnosperms, or whether a still more ancient point of origin for them must be looked for. Opinions differ as to whether they are to be considered as monophyletic or polyphyletic in their origin. Among the systematists who have dealt with their phylogenetic arrangement there are, in addition to many differences of opinion as regards matters of detail, two widely different viewpoints. The one school regards relative simplicity in the Angiosperm flower as primitive and places the group of families belonging to the Amentiferae and similar forms—they are nearly all woody—at the base of their system. The other school regards the spiral arrangement of parts, indefiniteness of number and general lack of economy in production, etc., as primitive and considers the Ranales as coming nearest to the pro-Angiosperms. Some argue that the earliest

Angiosperms were pollinated by insects, others do not favour this viewpoint. It is not my purpose, however, to attempt, at present, to add to these discussions, since the fossil record has, so far, failed to supply convincing evidence such as would settle the matters in dispute.

Through the study of modern ecology and plant distribution, particularly in the continent of Africa, I have been led to approach the problem from an entirely different standpoint. Africa is a continent with a very stable geological history, ever since Permian times. It has not changed very much throughout the long history of the Angiosperms. Now careful comparisons within all the narrower circles of affinity, within the limits of the families, or sometimes within the limits of the larger genera, have served to show that in Africa the moist warm tropical flora is older than the flora of drier and cooler regions. The tropical forest vegetation has apparently been differentiated under conditions which have remained unchanged for an enormous interval of time, indeed since the beginnings of the Tertiary, or earlier. This differentiation has been influenced, not by any pronounced changes in climate, but chiefly by the organic environment, competition for space, etc. The plant forms include trees, mostly hard wooded and not much branched, with relatively large and usually leathery leaves, varying in height, but otherwise of a rather uniform type; large numbers of lianes, passing from the woody types to the herbaceous; large numbers of epiphytes, representing a further and more specialised stage in evolutionary differentiation; and a considerable number of mesophytic undershrubs and herbs, which are associated with the forest as undergrowth.

The evidence from phylogeny, which I have recently been examining very fully for the world's flora as a whole, affords convincing support to the view that climatic differentiation has been responsible for the production of the types of plant form adapted to more open grassland conditions, to scrub, semi-desert, and desert, and also, though this began very early, to the temperate flora as well.

Past Changes of Climate

The view that the climate of the world remained more or less uniformly warm and moist from the beginnings of the Palaeozoic right down to the Pleistocene is now more or less definitely discarded. The more modern viewpoint, as expressed by Schuchert (1914), Brooks (1922) and others, recognises two great alternating types of climate. Following on periods of crustal movement and the formation

of large land areas, the general climate was cool with a marked zonal distribution of temperature, culminating, in at least four periods, in the development of great sheets of inland ice. During quiescent periods, on the other hand, the climate became warm and equable and apparently rather uniform over a great part of the world. The changes in Proterozoic and Palaeozoic times need not be dealt with, since the Angiosperms had not then appeared. In upper Jurassic times, when the earliest Angiosperms were undoubtedly already in existence, the climate of the world was warm. Schuchert points out that, at this time, the plants of Louis Philippe Land in latitude 63° S. are the same as those of Yorkshire. Whether this statement is strictly accurate or not, it can at least be said that they are very similar. Such warm conditions continued apparently for a period at least as long as the whole of the Tertiary, until the close of the Cretaceous, when there were many crustal movements, an upbuilding of mountain ranges and a lowering of temperatures. But there was no very extensive glaciation at this time—the only evidence of such is a local glaciation in the San Juan Mountains of Colorado—and the cooler interval was comparatively a short one. Most of the Eocene deposits, whether Lower, Middle, or Upper, indicate warm and equable conditions, and such prevailed at least through the first half of the Tertiary, or according to some authorities until towards its close, when the great ice period began to supervene.

Wegener's theory of drifting continents on a sub-fluid magma (1920, 1924) and consequent wandering of the poles and equator, while it helps to explain certain facts, yet tends to raise other difficulties. It is by no means easy to explain all the detailed phenomena of cooling and glaciation during Quaternary times on the lines adopted by Wegener. According to Wegener's theory, moreover, glaciation must always have been proceeding somewhere, unless both poles were surrounded by wide expanses of sea. This, as Brooks points out, is hard to reconcile with the extremely definite and limited glaciation which geological research has demonstrated.

Probably Wegener's theory will ultimately be combined with that recently put forward by Joly (1924) where the alternate periods of accumulation of heat and cooler conditions following on outbursts of volcanic activity and the upbuilding of mountain ranges and continents are explained by reference to the effects of the radio-activity of materials in the earth's crust. Nor is it likely that Wegener's theory can be applied in such a drastic way as he has been inclined to apply it.

THE IDENTIFICATION OF FOSSIL ANGIOSPERMS

Though Angiosperms from the Cretaceous onwards are abundant as fossils, yet from the palaeobotanical standpoint much of the material is unsatisfactory in so far as it consists mostly of leaf impressions. Several leading systematists have expressed the view that leaves, even living leaves, are, as a rule, altogether undeterminable. Nevertheless, palaeobotanists have not hesitated to apply the names of modern genera and even species to most of the fossil leaf impressions and, when occasionally they found themselves more than usually in doubt, they have suggested affinities by altering slightly the termination of modern names as *Celastrophyllum*, *Euphorbiophyllum*, *Populites*, *Sabalites*, *Leguminosites*, *Proteoides*, etc., or by using a prefix, as in *Palaeocassia*.

The number of fossil species belonging to modern genera would appear to have been extraordinarily great. Thus taking the North American species alone, from Knowlton's catalogue, we learn that somewhere about 180 species of *Ficus* are supposed to have been distinguished, together with about 40 species of *Cinnamomum*, 30 species each of *Celastrus* and *Celastrophyllum*, with another half-dozen species of *Celastrinites*, 100 or more species of *Populus* with numbers of *Populophyllum* and *Populites*, about 70 species of *Salix*, about 40 species of *Sapindus*, and 8 of *Sapindoides* with a few of *Sapindopsis*, about 60 species of *Myrica*, about 50 species each of *Aralia* and *Magnolia* and so on.

No botanist who has struggled with the many, often very polymorphic, modern species of *Ficus* can fail to admire the ingenuity of the palaeobotanists, who can distinguish two or three hundred species of the genus by leaf impressions alone. Scott, Seward and other distinguished palaeobotanists are not so confident and are inclined to approach the subject of the identification of fossil Angiosperm leaves with extreme caution. Berry (1914) who, with Knowlton and other American workers has done much to advance the subject, in discussing his own investigations on the Georgia Claiborne flora, says "The reference of *Arundo* to the grasses is positive, but in so far as its generic affinity is concerned the writer has simply conformed to palaeobotanical usage. The form classed as *Potamogeton* may not be a *Potamogeton*, although it resembles that genus very closely and is most certainly a monocotyledon of aquatic or semi-aquatic habit." And again (1924, p. 49) the same author remarks, "The use of the generic name *Arundo* is in a form sense and follows

usage. It cannot be claimed to have any especial significance as indicative of close botanical relationship."

While such palaeobotanical usages may be defended on the ground of geological convenience, from the purely botanical standpoint they are apt to give wrong impressions. The study of fossil Angiosperms, however, may be expected to pass through stages, familiar to all systematists. It is easier to increase the number of described species than to reduce them and sink a number of separately described forms in one. No doubt the time will come when a very large number of names of fossil species will be sunk as synonyms.

Some leaf forms are, of course, more characteristic and more easily recognisable than others and in several cases names given to leaf impressions have afterwards been corroborated by the discovery of specimens showing either flowers or fruits. This certainly tends to add to our confidence in the subject as a whole, in spite of the admittedly rash procedure of some palaeobotanists.

Some of the fossil flowers discovered have their structure fairly well preserved, e.g. the interesting monocotyledonous flower of liliaceous type, *Cretovarium japonicum* Stopes and Fujii, from the Upper Cretaceous of Japan, or *Combretanthites eocenica* Berry, and a few others, but it is hardly to be expected that mere impressions of flowers will yield much more definite information than those of leaves. Fruits are more often recognisable, since they are more easily preserved. Finally, we have the very important evidence from fossil Angiosperm wood. Relatively few Angiosperm woods have, so far, been described, but it is interesting, at the outset, to note that those that are known are nearly all of a tropical or subtropical type.

In drawing up a condensed general account of the Angiospermous fossil record, published figures and descriptions have had to be relied on, but these have been carefully consulted throughout. Accepting only the identifications that appear more or less well founded, we still have sufficient evidence to show that, before the end of the Cretaceous, the Angiosperms were very highly differentiated.

The Dicotyledons were, almost entirely, trees and shrubs and were proportionally apparently more abundant as compared with the Monocotyledons than they are even at the present time. Due value, however, should be given to the fact that woody types are more easily preserved than herbaceous, and dicotyledons than monocotyledons. The Archichlamydeae are predominant throughout among the fossil Angiosperms, but a few of the Sympetalae go back to the Cretaceous.

As already remarked, the fossil evidence does not throw much light on the rival theories regarding the origin of the Angiosperms. In support of those who favour Engler's arrangement, the Amentiferous families are very well represented at an early stage of the fossil record. The genus *Juglans* (the walnut) has existed apparently from the Middle Cretaceous to the present day. Formerly it was much more widespread than it is now. In the same family (Juglandaceae) the genus *Engelhardtia* has its characteristic winged fruits, as well as leaves, preserved. At present it is confined to South-East Asia, but during the Tertiary period species occurred in Europe and North America. The Myricales (bog myrtles) go back to the Middle Cretaceous. The genus *Myrica* throughout its geological history appears to have been—as it is now—a seashore (sand-dune) or else a rather distinctly hygrophilous type. The Betulaceae and Fagaceae are also ancient, the former being well-developed in the Upper Cretaceous of North America, and among the latter, the genus *Dryophyllum* (now extinct) being especially characteristic of the late Cretaceous and early Eocene floras of the whole world. According to Berry (1916, p. 81) *Dryophyllum* represents the ancestral stock from which the genera *Castanea*, *Castanopsis*, *Pasania* and *Quercus* took their origin, though that origin was in late Cretaceous times. The leaves of the various species of *Dryophyllum* were usually of a large simple coriaceous tropical-subtropical type.

Among the Urticales (Ulmaceae, Moraceae, and Urticaceae) the Moraceae, which at the present time are mostly tropical or subtropical, have the genera *Ficus*, *Artocarpus* and *Artocarpidium* going back to the Cretaceous.

Fruits as well as leaves of the breadfruit (*Artocarpus*) have been described by Nathorst (1890) from Greenland. According to Berry (1916) at least 15 fossil species are known. The genus *Ficus* is the largest fossil genus, including about 300 species altogether, but many are extremely doubtful as correct identifications. It appears first in the Upper Cretaceous. The elms (Ulmaceae) may be equally ancient, though their record is not so clear or certain. The Urticaceae are more herbaceous and are apparently a modern family. The fossil history of the Proteaceae has given rise to a voluminous literature, having been dealt with by Unger, Heer, Ettingshausen, Schimper, Schenck, Saporta and several others, as well as by more recent writers. Though modern members of the family are mostly South African and Australian, yet some do extend north of the equator in Australasia, Africa and America. Berry argues strongly for their former

occurrence in the northern hemisphere where, he thinks, they originated, appearing first in Lower Cretaceous times and becoming practically cosmopolitan in the Upper Cretaceous. Scott, on the other hand, gives it as his opinion (1924) that it is probable that the few genuine fossil Proteaceae are limited to Australia.

The occurrence of *Aristolochia* in the Upper Cretaceous beds of America and in the Tertiary of Europe is interesting as showing the early development of the climbing habit. Among the Centrospermae the Nyctaginaceae appear to have the most ancient fossil record.

Those who look upon the Ranales as the most primitive types of Angiosperm, connecting them with the Mesozoic Cycadophytes, can find equally good support for their views in the fossil record. The family Magnoliaceae are rich in supposed fossil remains from the Cretaceous onwards. About 60 fossil species have been referred to *Magnolia*. They are commoner in America than in Europe. The family Anonaceae, at present predominantly tropical, had the genus *Anona* in the Cretaceous of North America, but the genus *Asimina* goes back apparently only to the Eocene. The Lauraceae are supposed to include a very large number of somewhat uncertain leaf types, though fruits and seeds also occur. More than 50 fossil species of *Cinnamomum* have been described. The modern species of this genus are confined to the warmer regions, especially South-East Asia but they appear in the early part of the Upper Cretaceous in New Zealand, Australia, Central Europe, Greenland and North and South America. Such extraordinarily wide distribution of tropical types is very difficult to explain on the lines of Wegener's theory alone. The Eocene records of *Cinnamomum* include all the continents except the Antarctic and South America. According to Berry, the genus appears to have lingered as a common type in Mediterranean Europe until the changing climates that ushered in the Pleistocene caused its extinction.

Similarly the genera *Persea, Ocotea, Nectandra, Sassafras* and *Laurus* are also said to go back to the Cretaceous and to have been widespread, though at the present time they are mostly confined to the warmer regions of the world. The genus *Sassafras* is important because its peculiar lobed leaves and characteristic venation are very distinctive and make it easily recognisable. Existing species of *Sassafras* occur in North America and South-Western China but more than 40 fossil species have been described. At the base of the Upper Cretaceous the genus ranged from Greenland to South America.

Among the Rosales, the witch-hazel family (Hamamelidaceae) have the genera *Hamamelis* and *Parrotia* from the Cretaceous and *Liquidambar* from the Eocene beds of North America. The Leguminosae, though recorded for the Cretaceous, become abundant only in the Eocene. A phyllode-bearing *Acacia* (*A. wilcoxensis*) is described by Berry for the Wilcox (Eocene) beds. Other Wilcox genera include *Inga, Pithecolobium* and *Mimosites* of the Mimosoideae, *Cassia, Caesalpinia, Gleditschiophyllum* of the Caesalpinoideae, and *Sophora, Dalbergia, Canavalia* of the Papilionatae.

The Platanaceae (plane trees) have flowers and fruits as well as leaves recorded from the Cretaceous. The globular catkins are easily recognisable and have been found in the Cretaceous beds of Bohemia. The Aceraceae (maples) also have leaves and fruits in the Middle Cretaceous of North America. The family Anacardiaceae are best represented in the fossil record, as they are at present, by the genus *Rhus*, which is said to go back to the Upper Cretaceous, as also the genus *Pistacia*. In the Ilicaceae, the genus *Ilex* has more than a hundred fossil species, of which about a dozen are Upper Cretaceous. The Celastraceae have five genera in the Cretaceous and become very important in most fossil floras of the Tertiary. The genus *Celastrus* is the largest fossil genus and at one time was apparently cosmopolitan. The genus *Elaeodendron*, now confined to South Africa, had four Upper Cretaceous species, one from Australia and three from North America. The Sapindaceae, at present one of the most characteristic of the woody tropical and subtropical families, also go back to the Upper Cretaceous of North America, Greenland and Bohemia. The Rhamnaceae are equally ancient. Among the Sterculiaceae, the genus *Sterculia* was apparently well represented in the Upper Cretaceous.

The Myrtaceae are divided into the subfamilies Myrtoideae, with fleshy fruits, widespread in the tropics of both worlds, and the Leptospermoideae, with capsular fruits, mainly Australian. The genus *Eugenia* with 600–700 species is the largest in the Myrtoideae, the genus *Eucalyptus* in the Leptospermoideae. Now there is little doubt that *Eugenia* is a very ancient type. It is recorded for the (Dakota) Cretaceous beds of North America, and Cretaceous fossil wood from Natal described by Warren (1912) was found to be practically identical with the wood of the modern *Eugenia cordata*, a common subtropical very hygrophilous Natal tree. The evidence for *Eucalyptus* being equally ancient is much more doubtful. It has been recorded for Europe in Cretaceous times by Heer, Unger and Ettingshausen, and

Scott (1924) accepts the evidence as well attested (giving a figure of *Eucalyptus angusta* which shows flowers as well as leaves) yet Berry (1916) says that all the numerous Cretaceous fossil plants from North America now referred to *Eucalyptus* show characteristic features of *Eugenia* or the closely allied genus *Myrcia*. The evidence, from phylogeny and present-day distribution and all that so far has been brought to light regarding the course of ecological differentiation, would certainly support the view that *Eucalyptus* is a derivative type.

The Combretaceae, a rather characteristic family of drier subtropical regions, are not recorded earlier than the Eocene. Many apparently Araliaceous fossil leaves have been referred to the genus *Aralia*. No fewer than 50 species are supposed to go back to the Cretaceous. The genus *Panax* is also recorded for Greenland, North America, and Bohemia. Fifteen species of *Hedera* have been described for the Cretaceous of America and Europe. In the Cornaceae, the genera *Cornus* and *Nyssa* are as old as the Cretaceous. The Umbelliferae, on the other hand, are apparently modern. All the families so far mentioned belong to the Archichlamydeae and they are by far the most abundantly represented.

The Sympetalae are not so common, but they do occur even in the Cretaceous. The Myrsinaceae at present are predominantly tropical. Of the 75 fossil species of *Myrsine* seven or eight go back to the Cretaceous, mostly in America, but one occurs in Europe. Among the Sapotaceae many Cretaceous fossils both in Europe and America have been referred to the form genus *Sapotacites*, but *Mimusops* is also said to be nearly as ancient. In the Ebenaceae, the genus *Diospyros* has 180 existing and nearly 100 fossil species, no less than 17 being traced back to the Cretaceous, occurring in localities as widely separated as Australia, Bohemia, Greenland and Vancouver Island; another striking instance of wide distribution. The genus *Royena* is represented by fruits from the oasis of Chargeh in Egypt (Upper Cretaceous). Among the Oleaceae, leaves of the ash (*Fraxinus*) are recorded for the Upper Cretaceous of Greenland. The Apocynaceae, another modern tropical family, occur in the Cretaceous as species of *Apocynophyllum*. The genus *Nerium* was also recorded by Saporta from the Upper Cretaceous of Westphalia, but Berry considers this a mistake, the genus in question being a member of the Myrtaceae and not *Nerium*. In the Boraginaceae the genus *Cordia*, an admittedly primitive phylogenetic type, at present tropical or subtropical, appears to go back as far as the Cretaceous in America. The bulk of the family is relatively modern. Among the Caprifoliaceae the genus

Viburnum has been recorded from the Cretaceous of Greenland and North America. Many other families, which we have not mentioned, go back as far as the Eocene.

Among the Monocotyledons, the palms were common during the Cretaceous and still more so throughout the Tertiary. Their cosmopolitan distribution as fossils contrasts once more with their restricted, mostly tropical or subtropical, distribution at the present time. Their wood is frequently well preserved from the Cretaceous onwards. The evidence for the occurrence of the grasses is more uncertain, though the reed grasses *Arundo* and *Phragmites*, or types like them, occurred in the Cretaceous of Greenland and North America. Of the Typhaceae *Sparganium* appears to be equally ancient, fruits as well as leaves being preserved. Among the Araceae the aquatic genus *Pistia* is found in the Upper Cretaceous beds of North America and Europe. In the Liliaceae leaves that have been referred to the climbing genus *Smilax* are found in the Upper Cretaceous of Bohemia. The genus *Dracaena* and other arborescent forms are found in various Tertiary beds. On the whole, however, the Monocotyledons are poorly represented and the fossil evidence throws no light on their origin or on their relationship to the Dicotyledons.

THE ECOLOGICAL INTERPRETATION OF THE FOSSIL ANGIOSPERM RECORD

Ecological deductions from the fossil Angiosperm record have usually been made to depend on the assumed correctness of the identifications. Arguments have then been based on the known ecological behaviour of modern representatives of the same genera or species. In many cases and with due precautions, as we have seen, this procedure is doubtless perfectly justifiable. At the same time, it does admit of much destructive criticism from those who do not believe that the majority of fossil Angiosperm leaf impressions are recognisable or capable of being referred to modern genera.

This difficulty, however, from the purely ecological standpoint (which is the important one when past climates and their relationship to plant distribution are being considered) can to a large extent be avoided by adopting another line of procedure. Morphological comparisons of the Angiosperm fossil plants can be made, not with modern individual genera or species, but with modern types of vegetation. To do so successfully, statistical methods must be adopted.

The credit of introducing ecological statistical methods in determining the climatic relations of floras is due particularly to Raunkiaer.

His system of classifying the life forms of plants is now well known, thanks largely to an explanatory article by W. G. Smith which appeared in the first number of the *Journal of Ecology* (1913). It is, of course, difficult to apply Raunkiaer's actual system to fossil plants, since, with very few exceptions, they all belong to his one class of Phanerophytes (Trees and Shrubs) and the fossil record gives little information regarding the relative size of the woody plants to which the leaves belonged. The abundance of trees and shrubs, after making due allowance for their greater likelihood of being preserved, shows that the climate of most parts of the world, from the beginning of the Cretaceous and earlier right down to the close of the Tertiary, was what Raunkiaer calls a "Phanerophytic climate."

This does not, of course, mean that there were no herbs, any more than a phanerophytic climate implies a total absence of herbs at the present time.

Statistical Comparisons; Leaf Size

The Phanerophytes were originally subdivided by Raunkiaer into evergreen and deciduous classes and further, according to the degree of protection of the renewal buds, depending on decrease in size of the whole plant. The majority of the fossil leaves appear to have been of the evergreen type, though it is not always easy to be certain on this point. In later papers Raunkiaer gave attention to variations in leaf size. The most satisfactory method of doing so is to estimate the average total area of the surfaces of the individual leaves of each species. When very large numbers are being dealt with, however, and especially when published descriptions have to be relied on, the calculation of leaf areas becomes very laborious. Some published descriptions omit reference to leaf size altogether or use vague general terms, but usually the average length and the average width in the widest part are given. A rough idea of leaf size can be obtained from such linear measurements.

In statistics dealing with the South African flora (Bews, 1925), four main classes of leaves were recognised—(*a*) simple leaves over 3 in. long, (*b*) simple leaves 3–1 in. long, (*c*) simple leaves less than 1 in. long, and (*d*) compound leaves. Average measurements were taken in each case and the English linear system of measuring was adhered to since it is used throughout the *Flora Capensis*. Apart from this, however, the three sizes (3 in. or 7 cm., 3–1 in. or 7–2½ cm., and less than 1 in. or 2½ cm.) have proved very convenient.

In order that the fossil flora may be compared as regards leaf size with modern types of vegetation, statistics of the same nature have been compiled from various published monographs and these are set forth in Table I. Only the more extensive monographs have been made use of, since, where less than 50 fossil species have been described, the numbers have been considered too few to yield statistical percentage results which can be compared with modern floras.

TABLE I

Fossil Angiosperms

Locality and geological horizon	Authority	Total No. dealt with	Leaves simple over 3 in. %	Leaves simple 3–1 in. %	Leaves simple under 1 in. %	Leaves compound %
Eastern Gulf region Upper Cretaceous	Berry	138	54	29	7	10
South Carolina Upper Cretaceous	Berry	50	64	18	6	12
Laramie, Denver Upper Cretaceous	Knowlton	75	57	26	3	14
Wilcox group Lower Eocene	Berry	262	47	17	5	31
Claiborne flora Middle Eocene	Berry	58	62	10	2	26
Jackson flora Upper Eocene	Berry	89	57	16	4	23

While the statistics given in Table I do not depend on the identifications of the species concerned, yet they still have faults due to the necessary imperfections of the fossil rccord. One or two of these may be referred to briefly.

(*a*) The preserved specimens may not represent average samples of the species to which they belonged. It is well known that young leaves differ from old, juvenile forms from the adult, leaves on coppice shoots from those on main stems or branches, shade-leaves from sun-leaves. This difficulty must always be kept in mind when individual identifications are being considered, but statistical methods and percentages of fifty or more are not likely to be affected much by some specimens being non-typical of the species to which they belonged.

(*b*) The percentages of compound leaves as given in the table do depend, to some extent, on the accuracy of their supposed determinations. Compound leaves are only occasionally preserved complete and usually only separated leaflets occur, especially in the case of pinnate leaves. Of course their exact relationships may be in doubt and still they may be recognised as at least being compound-leaved forms. The matter is not of any great importance.

(*c*) The most serious difficulty in the ecological interpretation of the fossil record and in seeking to correlate past climates and vegetation lies in the fact that the whole preserved collection of fossil leaves in any particular place may not have been, and indeed very likely was not, typical of the vegetation as a whole. The leaves of trees and shrubs would be more easily preserved than those of herbs, the vegetation of stream banks, river banks and estuaries would be more likely to be found abundantly than the vegetation of drier areas away from water, mesophytic or hygrophilous types would naturally be more common as fossils than extreme xerophytic types.

The importance of this difficulty has been generally recognised and, if anything, has been perhaps over-emphasised. It is unnecessary to go to extremes and declare that because the fossil record is incomplete it is, therefore, worthless; that because the vegetation of desert regions would not be so easily preserved, therefore its absence from the fossil record not only makes it possible but even probable or practically certain that desert types are just as ancient as the mesophytic types which do occur so abundantly. Caution is a very desirable thing, but it can be carried too far. We can continue to interpret the past in terms of the present, and our safest guide is what can be learned from the ecological behaviour of modern types of vegetation. Experience gained in dealing with the ecology of the subtropical vegetation of South Africa has shown, beyond any doubt, that even in the hygrophilous habitats mentioned (stream banks, river banks, lagoons and estuaries) a dry climate is not without a pronounced and easily recognisable effect. I have dealt with this question in detail elsewhere (1925). It is true that along stream and river banks hygrophilous trees and shrubs can extend into drier climatic areas, but even in such situations the effects of increasing aridity are soon apparent. South African tree types like *Xymalos*, *Bridelia*, *Macaranga*, *Voacanga*, *Rauwolfia*, *Eugenia cordata*, etc., which are closely similar to the average form found abundantly as fossils from the Cretaceous onwards, occur along streams, it is true, but only in the moister and warmer climatic areas. In the drier areas, they are replaced by quite different types like *Acacia*, *Rhus*, *Zizyphus*, *Combretum*, etc., which also grow along the stream and river banks in such areas.

If the climates of Cretaceous and Eocene times had been as dry as the climate of, say, the South African Karroo is now, there appears to be no reason why the woody vegetation of the river banks and estuaries and the preserved fossils should not have recorded the fact.

Since herbaceous forms have not been commonly preserved, we shall compare the fossil types only with modern trees and shrubs. To enable us to reach conclusions so far as leaf size is concerned similar statistics for modern types of vegetation are given in Table II.

TABLE II

Modern Trees and Shrubs

Ecological type	Total No. dealt with	Leaves simple over 3 in.	Leaves simple 3–1 in.	Leaves simple under 1 in.	Leaves compound
		%	%	%	%
South Africa as a whole	800	20	40	9	31
South African hygrophilous subtropical type	60	75	19	0	6
South African mesophytic forest type	150	32	47	3	18
South African xerophytic parkland and scrub types	500	11	34	13	42
British temperate type	100	20	36	28	16

The figures given in Table I show that the early Angiosperms while exhibiting a fair amount of differentiation as regards leaf size were predominantly of a large-leaved type and comparison of the two tables shows that the Cretaceous and Eocene vegetation approached nearest to modern warm moist (hygrophilous) forest vegetation. The percentage figures show that the early vegetation differed markedly from the modern xerophytic scrub vegetation or open parkland vegetation on the one hand and from modern temperate woody vegetation on the other. I have shown in my work on *Plant Forms* (1925) already referred to, that the South African xerophytic scrub and "Tree Veld" vegetation is to be considered relatively modern and derivative, basing my conclusions on the evidence from phylogeny and modern distribution. The fact that there is a marked increase in the percentage of compound-leaved forms in such derivative vegetation may be significant and it is, therefore, worth noting that the percentage of such compound-leaved forms in the fossil record is higher in the Eocene than in the Cretaceous.

LEAF MARGINS

While leaf size is one of the most important features to be correlated with climate, there are other characters, which are also worthy of attention. Bailey and Sinnott (1915) are quoted by Berry (1916, p. 138) as having formulated a method of approximating climatic factors by a study of the percentages of dicotyledonous leaves with entire and with toothed margins. The Wilcox flora, which is the richest in records, in so far as it is represented by leaves and leaflets,

comprises 264 species with entire and 64 species with toothed margins, or 82·6 per cent. of the former and 17·4 per cent. of the latter. This percentage of entire-leaved forms shows remarkably close agreement with various modern tropical floras e.g. Ceylon (80 per cent.), Manilla (81 per cent.), West Central Africa (81 per cent.), Queensland (82 per cent.), New South Wales (82 per cent.) and Florida (83 per cent.) but differs entirely from modern temperate floras. The British temperate trees and shrubs, for instance, only have about 30 per cent. with entire leaves. It is, of course, not so obvious why a simple character like toothed margins should depend on climate, but if it does not depend directly on climate, but rather on phylogenetic history independently of the influence of the environment, it is all the more valuable as an indication of the ancient character of the tropical tree form, which, in this respect as well as others, agrees so closely with the ancient fossil Angiosperms.

Leaf Texture

Berry (1914, p. 67) calls attention to the presence of numerous fossil Angiosperms with coriaceous leaves, and says that this is believed to be due to insolation and the pseudo-xerophytism of swamp habitats rather than to any approach to aridity. As a matter of fact, however, the leaves of most evergreen species of trees, even when they grow in the moistest types of tropical rain forest, show some degree of leathery texture and are only rarely quite thin and membranous. Species with coriaceous leaves are by no means confined to swamp habitats. *Xymalos monospora*, for instance, is a dominant hygrophilous Natal tree with distinctly coriaceous leaves. It is found in the wettest types of forest and nowhere else, but the soil in which it grows is well enough aërated and the character of its leaves, as in the case of many other similar species, cannot be explained by any theory of physiological drought or pseudo-xerophytism. Coriaceous-leaved species are, of course, also found under drier conditions and it is not denied that this leathery texture may be looked upon as a xerophytic response. The term "xerophyte" is one which often leads to misapprehensions. It is sometimes used purely in a morphological sense, sometimes, on the other hand, it is applied to habitat as well. Now the possession of coriaceous leaves does not necessarily imply dry conditions and if they occur abundantly in situations where plenty of water is available, it is clear that an explanation must go deeper. It is not enough to talk vaguely of xerophytism.

It seems to me that a considerable amount of light is thrown on the subject by considering more carefully the whole question of the water supply of the leaves and its relationship to the water-conducting power of the wood. Farmer (1918) devised a method of measuring what he called the "specific conductivity" of woods and showed in a general way that evergreen species are less efficient in raising water quickly to their leaves than are deciduous species. In Natal, recently, we have applied his method to a considerable number of species and gradually it has become apparent that increased efficiency in water conduction has only been reached by dicotyledonous trees after a long period of evolutionary development. The relatively primitive evergreen tropical or subtropical forms are, as a rule, not able to pump up water very quickly. Moreover, further experiments on the rates of drying out of their leaves and on their "water deficits" under varying conditions have shown that some of them begin to suffer after only brief periods of bright sunshine and relative aridity. Though plenty of water may be available at their roots, it cannot be supplied rapidly enough to their leaves. Such species, of which *Xymalos monospora* is an example, are, therefore, confined to the wettest areas and, even there are occasionally in danger. Hence probably the necessity for having coriaceous leaves. Even tropical rain forest is not uniformly and continuously equally moist. There are short, dry intervals and leathery-leaved trees are characteristic, especially in the upper canopy.

Some coriaceous-leaved trees, which have low rates of water conduction, occur, not only in wet forest, but in drier places as well. These show greater powers of withstanding a lowering of the leaf water content. *Ptaeroxylon utile* is a good example of this class.

Finally, the more derivative, more highly evolved species of trees which occur in drier subtropical areas or in colder (temperate) regions often have thin membranous leaves, but, at the same time, show a much higher rate of water conduction. Such forms tend to be more or less regularly deciduous in regions where a pronounced resting season is brought about either by dry conditions (dry winters) or by cold conditions (cold winters).

The figures given in Table III are selected from numerous experimental observations made on the Natal flora and on exotic species cultivated there.

TABLE III

Water Conduction in Trees[1]

Tropical or subtropical mesophytic or hygrophilous evergreen types	Spec. conductivity	Xerophytic subtropical or temperate deciduous types	Spec. conductivity
Podocarpus henkelii	12–16	*Magnolia* sp.	20–40
Xymalos monospora	10–17	*Platanus occidentalis*	38–75
Eugenia cordata	12–13	*Amygdalus persica*	35–66
Avicennia officinalis	17–21	*Heteromorpha arborescens*	27–56
Rhamnus prinoides	12–19	*Ficus capensis*	70–80
Gardenia globosa	19–25	*Cordia caffra*	50–90
Ptaeroxylon utile	10–22	*Maesa rufescens*	80–100

The differences in the rates of water conduction between the leathery-leaved evergreen types and the thin-leaved or deciduous types are sufficiently striking and in general it would appear that the coriaceous texture of leaves in moist-tropical species is probably to be explained by their relative inefficiency in water conduction. The significance of the presence of so many coriaceous leaves among fossil Angiosperms is, therefore, two-fold. (1) It serves to connect the earlier types of plant with tropical or subtropical modern hygrophilous or mesophytic types, as before, and (2) it is not necessarily to be explained by the pseudo-xerophytism of swamp habitats or by any marked approach to aridity but simply by the same lack of efficiency in the water-conducting power of the wood which is found to-day in tropical forms. It is reasonable to suppose that in such basic physiological processes, as in other connections, evolutionary development has gradually led to increased efficiency.

STRUCTURE OF THE WOOD

With fossil forms, of course, it is impossible to carry out experiments on the rates of water-conduction, but their woods are to some extent available though relatively few examples have so far been described. As in the case of the leaves, the giving of the names of modern genera or species to fossil woods, the determining of their systematic positions and relationships to modern forms is a difficult matter and is not necessarily the most important task to be undertaken by the palaeobotanist. Apart altogether from their identification, much may be learned from a careful study of their structure and by ecological comparisons with modern types. Unfortunately, very little work of this kind has so far been done.

The oldest known fossil dicotyledonous woods are of Lower

[1] The figures have been taken from unpublished results obtained partly by Dr R. D. Aitken and partly by Miss Sheila Maritz.

Cretaceous age and have been described by Dr Marie Stopes (1913, 1915). There are five genera with one species in each. In four of them, *Aptiana radiata*, *Cantia arborescens*, *Sabulia scottii*, and *Hythia elgari*, the rather small vessels, which vary from 20–70μ in diameter, would suggest that water conduction was not very efficient, but the fifth, *Woburnia porosa*, has large vessels 350μ in diameter. The last mentioned, however, agrees in structure with the tropical Dipterocarpaceae. Some tropical species, especially those which tend to become lianes, do have large vessels. Fairly extensive experiments carried out in Natal have shown us that the rate of water conduction is not to be correlated merely with the total area of the lumina of the conducting elements, in proportion to the whole area of the woody stem in cross-section. The rate of water conduction also depends on the nature of the conducting elements themselves and particularly on the characters of the pits, pores or perforations connecting the separate elements with one another. There is room for much further work on woods from the standpoint of efficiency.

The affinities of the other Lower Cretaceous fossil woods described by Dr Stopes are undetermined, though, according to Scott (1924), *Aptiana* has been confidently placed in the family Ternstroemiaceae (to which the familiar coriaceous-leaved Camellias belong) by two Dutch writers, Profs. Janssonius and Moll.

Other woods of Upper Cretaceous age have been described from Japan by Stopes and Fujii and by American writers from North America. Their affinities with relatively primitive hygrophilous or tropical families are indicated in a general way by the names that have been assigned to them (*Saururopsis*, *Jugloxylon*, *Populocaulis*, *Fagoxylon*, *Sabiocaulis*, *Dombeyoxylon*, *Laurinoxylon*, *Ficoxylon*, *Ulmoxylon*, *Perseoxylon*, *Elaeodendroxylon*, *Ebenoxylon*); but the total number that have been described is very small as compared with the large numbers of leaf impressions that have been dealt with.

The fossil woods should be studied, not only as regards their conducting elements and probable efficiency in water conduction, but also as regards the development of medullary rays and other parenchymatous storage tissue in response to the necessity for providing for a resting season. Tropical woods from moist regions are usually hard-woods. Softer woods are produced in regions where dry or cold seasons lead to a more or less prolonged resting season. Indeed the morphological changes brought about in woody species by the advent of seasonal climatic differentiation (the alternation of a favourable warm moist growing season with an unfavourable dry

or cold resting season) are very varied and are of the utmost importance in any analysis of the course of ecological evolutionary history.

From this standpoint, attention has been directed to the presence or absence of well-marked annual rings, though this is only one, and in many ways not the most important, feature to be studied. There are growth rhythms in plants growing under more or less uniform and continuously favourable conditions which may be, to some extent, independent of external climatic changes, and successive rings of growth in woody stems may not be annual or even seasonal rings.

The presence or absence of clearly marked annual rings is not of course to be neglected (and in the fossil woods described they are not, as a rule, well marked) but in seeking to correlate ecological behaviour with climate there are many other morphological features to be taken into consideration as well. Until more work is done on the subject, however, it is impossible to draw any more definite conclusions than those tentative ones outlined above.

In conclusion, it may be said that the fossil evidence as regards the past history of the Angiosperms, incomplete and unsatisfactory though it is in many respects, yet, when its more general features are analysed, does lend strong support to the view that warm moist conditions were, for a very long period, much more widespread than they are now, and further, that the early Angiosperms were similar ecologically to the types now found in moist tropical and subtropical areas. They were differentiated in the same way as modern tropical mesophytic floras but they showed only slight indications of the influence of drier or colder conditions.

The fossil evidence, therefore, so far as it goes, supports the views already outlined, which depend primarily on the study of the phylogeny and distribution of modern vegetation. The whole subject of the ecological evolutionary history of plant forms, I am convinced, is full of very interesting possibilities.

Summary

1. The study of fossil Angiosperms has made considerable progress during recent years, particularly through the work of Berry, Knowlton, and others in America. Most of the fossil remains consist of leaf impressions and the determining of their exact affinities must always be difficult. The fossil evidence has not as yet thrown much light on various rival theories regarding the origin of the Angiosperms. A condensed account is given of the identifications that appear more or less well founded.

2. In seeking to correlate the fossil record with past climates, ecological comparative methods are adopted and the fossil remains are compared in groups statistically with modern types of vegetation.

3. The features selected for comparison are (i) leaf size, (ii) leaf margins, (iii) leaf texture, (iv) structure of the wood, and in each case it is shown that the earlier fossil Angiosperms were closely similar to the types now occurring in moist tropical and subtropical areas.

4. The ecological interpretation of the prevalent coriaceous texture in the leaves of both fossil and modern tropical trees is discussed with reference to experimental work carried out in Natal on the water relations of various species. Leathery texture and a certain degree of "xerophytism" generally in the leaves of many ecologically primitive types of tropical hygrophilous trees are correlated with relative inefficiency in their power of water conduction through the wood.

NOTE. The manuscript of this chapter was submitted to Prof. Seward, and I am much indebted to him for certain helpful criticisms. It is only fair to add that with regard to the identification of the fossil Angiosperms he is inclined to adopt even a more cautious attitude than I have found necessary. The statistics and comparisons given in the later chapters of the book are not, of course, much affected, since they do not to any great extent depend on identifications.

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CHAPTER II

THE ARCHICHLAMYDEAE

Introduction

If we adopt the most general viewpoint possible and deduce nothing more from the fossil Angiosperm record than that from Cretaceous times onwards the preserved remains of flowering plants indicate general widespread warm and moist climatic conditions, it seems perfectly reasonable to suppose—at least as a working hypothesis—that, at the present time, ancient types will be found in regions that are still warm and moist and have remained so, as far as geological evidence shows, for a very long period of time. This does not mean that the whole moist tropical flora is of an ancient type. Differentiation does go on under relatively unchanging conditions, as is sufficiently shown by the evolution of life in the sea. Such differentiation may partly be considered to be due to internal forces and thus partly may be entirely independent of the external environment, but in warm, moist, tropical regions, where conditions of life are very favourable, the effect of the living environment (plant competition for space, etc.) is also very important. The latter, of course, acts partly through modifying the inorganic environment, particularly through alterations in the light factor. The animal world, especially the insect world, has also played a part in connection with floral evolution, and in some directions, particularly in the more superficial flower characters, and in types which play a subordinate rôle in the vegetation, this has, in a few cases, proceeded even further in the moist tropics than among allied types in drier subtropical or extratropical regions.

In connection with their vegetative life, tropical plants have become differentiated in various directions. The tree forms vary in height and, to some extent, in the characters of their wood, their bark, their branching and their leaves, though on the whole remaining of a fairly uniform, tall, hard-wooded, sparingly branched, large-leaved, often leathery-leaved type. The climbing habit appeared very early as is shown by the abundance of woody lianes in many ancient orders and families as well as by the fossil record. The lianes also show progressive evolutionary development from woody

types to herbaceous. The herbaceous habit in general is also ancient, as exhibited by the herbs occurring as forest undergrowth and around the forest margins and spreading along river banks and streams.

Minor evolutionary lines of development have resulted in the production of epiphytes (which in many cases connect with the lianes), parasites and saprophytes and families of insectivorous plants.

Emphasis should be laid on the fact that the great lapse of time has allowed the internal forces which influence evolutionary differentiation to produce the various families of flowering plants which (with a number of notable exceptions) are all well represented in the moist tropics. It is true that the general ancient character of the moist tropical flora is shown by such facts as the following:

(*a*) The relatively primitive Archichlamydeae are proportionately much better represented in the tropics than the relatively advanced Sympetalae.

(*b*) Nearly all the great tree families of the Angiosperms are predominantly tropical.

(*c*) Most of the orders recognised as primitive by different schools of thought among systematists are either tropical or, if they extend into extratropical regions, are hygrophilous or show traces of a tropical ancestry. This applies to the Piperales, Salicales, Juglandales, Myricales, Fagales, Urticales, Ranales, Pandanales, Helobieae and Principes.

But from our present standpoint comparatively little useful information is brought to light by attempts to trace the general phylogeny of the Angiosperms as a whole or to seek for connections between the more clearly defined orders and families. Such general phylogenetic schemes must remain, at the present stage of our knowledge to a greater or less extent speculative.

If, however, we accept the assumption that through the long history of the Angiosperms their natural groups have become differentiated, partly through what Osborn has described as the action, reaction and interaction of internal forces, and partly through the similar action, reaction and interaction of the surrounding plants and animals (the biota), and suppose that the physical environment, because of its relative uniformity had, to begin with, comparatively little effect, then, in our study of phylogeny, we are led to confine our attention, for the most part, to the various narrower circles of affinity, to the families or the best defined orders.

Within such narrower circles of affinity the evidence that the moist tropical flora is older than the flora of drier regions, on the

one hand, and of colder regions, on the other, is quite strong and it will be dealt with in detail in the pages which follow. That the extreme climatic differentiation, which began apparently during the latter half of the Tertiary or perhaps only towards its close, has been responsible for the evolution of plant forms adapted to modern dry or cold regions is a perfectly reasonable supposition, but it is not denied that, in many cases, the process began much earlier. The period of lowering of temperatures at the close of the Cretaceous doubtless saw the beginnings of many derivative temperate types. But the fact that it is only within the narrower circles of affinity that, as a rule, it can be shown that the moist tropical types are phylogenetically older than the drier or colder types is very significant.

THE ORDERS AND FAMILIES OF ARCHICHLAMYDEAE

The evidence supplied by phylogeny is evidence which is somewhat difficult to present. Systematists have, on the whole, succeeded wonderfully well in bringing like near to like and in separating types which are fundamentally different, but they have seldom tried to explain the underlying principles that have guided them. We must accept the arrangements and subdivisions that have been arrived at by the various specialists who have dealt with the different families and assume that, so far as the families themselves and the more natural of the orders are concerned, these arrangements are as natural as is possible at the present stage of our knowledge. Our task is easier since we are only concerned with the narrower circles of affinity, and the relationships between the main orders and their arrangement in a general phylogenetic scheme, from our present standpoint, is of less importance. An effort, however, must be made to cover the whole ground, since, though it is easy to select examples which support our theory, selected evidence must always remain unsatisfactory and unconvincing.

Since it is not considered particularly important what scheme of arrangement of the families is followed, Engler's system is adhered to more or less closely. The new system proposed by Hutchinson (1926) has also been consulted, but interesting though the ideas there set forth are, it may be doubted whether the great stress laid on the difference between the woody and herbaceous habit is quite justifiable. While the general evolutionary trend has been from the woody to the herbaceous, yet the fact that the herbaceous habit can arise quite easily within very narrow circles of affinity, even within the limits of a genus, must always be kept in mind.

The numbers of genera and species included in each group are given in each case but are, of course, only to be taken as approximately correct.

DICOTYLEDONS (8000 genera, 120,000 species): ARCHICHLAMYDEAE (4500 genera, 68,000 species).

The orders belonging to the Monochlamydeae, which are dealt with first by Engler, may or may not be among the most primitive of Angiosperms. As already explained, I do not propose to deal with such questions in detail, but merely to refer to such facts as have a direct bearing on ecological evolutionary history.

The first half-dozen or so of Engler's orders are small and somewhat isolated and, consequently, do not throw much light on our problem. Yet, even among them, certain facts are significant.

SALICALES (2 gen., 200 sp.). The two genera *Populus* and *Salix* are among the earliest known fossil Angiosperms and, at the present time, both favour stream and river banks. According to Laurent (1907) it is always the types of warm climates which are the oldest.

MYRICALES. The only genus *Myrica* (60 sp.) is as old as the poplars and willows and, like them, at the present time, with few exceptions, favours hygrophilous habitats.

JUGLANDALES (6 gen., 40 sp.). Also go back to the Cretaceous; at present distributed over tropical Asia and North temperate regions. The fossil types are nearest to the tropical forms.

FAGALES. Betulaceae (6 gen., 80 sp.) (birch, hazel, hornbeam, alder) and the Fagaceae (5 gen., 350 sp.) (oak, beech, chestnut).

In these families, which include so many of the present day temperate deciduous trees, there are indications that the older phylogenetic forms are the evergreen types of warmer regions. The northern deciduous oaks, for instance, tend to be evergreen in their juvenile forms. Jeffrey (1917) on grounds of comparative anatomy looks upon the evergreen forms as the older. Berry (1916, p. 81) looks on the fossil genus *Dryophyllum*, which was world-wide in Cretaceous times, as the ancestral stock from which the genera *Castanea*, *Castanopsis*, *Pasania* and *Quercus* were derived. The leaves of *Dryophyllum* were apparently usually of the rather large, coriaceous, evergreen tropical type.

PIPERALES. The Piperaceae (9 gen., 1100 sp.); Chloranthaceae (4 gen., 35 sp.) and Lacistemaceae (1 gen., 15 sp.) are tropical forest families; the Saururaceae (3 gen., 5 sp.) are mostly swamp plants. Their habitats are, therefore, all of a primitive nature, but considerable differentiation in the direction of the herbaceous

habit has taken place. Some authorities regard the order as very primitive.

URTICALES. Moraceae (60 gen., 1000 sp.), Cannabinaceae (2 gen., 3 sp.), Urticaceae (43 gen., 600 sp.) and Ulmaceae (15 gen., 130 sp.).

In this order the Moraceae consist mostly of trees and are relatively more tropical and more primitive than the allied Urticaceae, which are mostly shrubs and herbs and are more widely distributed. The small, herbaceous family, the Cannabinaceae are obviously derivative and include the hop, *Humulus lupulus* and the widespread weed *Cannabis sativa.* Within the Moraceae, while the majority are tropical, the Artocarpoideae show advance in their complicated receptacles and curved or inverted ovules, and include the large genus *Ficus*, which, though it has a very ancient fossil record, in its modern forms includes species, which have spread into drier and colder regions, and shows a considerable amount of ecological differentiation, including epiphytic species and low-growing suffruticose forms. In the Ulmaceae the drupaceous-fruited Celtidoideae have sometimes endosperm and are more primitive than the winged-fruited Ulmoideae, which have no endosperm. While both tribes extend into temperate regions, the former is, on the whole, distinctly more tropical or subtropical than the latter.

PROTEALES. The Proteaceae (55 gen., 1000 sp.) are a very interesting but somewhat isolated family of uncertain affinities. They are mostly South African and Australian with a few representatives elsewhere, e.g. New Caledonia and South America. In the southern hemisphere their present day distribution is chiefly warm temperate with extensions northwards along the mountain ranges into tropical regions and they may represent a very early type of temperate flora. There are several other families which indicate that the first responses to temperate conditions took place on the mountain ranges of the world, and it is interesting to note that the African mountain ranges are very old, going back to Permian times. According to Engler's arrangement, the Proteales connect with the Santalales; Hutchinson thinks they are allied with the Thymelaeaceae; Balfour was of the opinion that they had affinities with the Rosales (Leguminosae).

SANTALALES. The Olacaceae (27 gen., 160 sp.) are floristically the most primitive in this order and they are a family of tropical trees and shrubs. Hutchinson looks on the "Olacales" as connecting the "Santalales" with the "Celastrales." The Grubbiaceae (*Grubbia*, 4 sp.) are allied, but more advanced Cape heathlike plants—like the Proteaceae, probably an ancient, warm temperate, derived type. The

Santalaceae (26 gen., 250 sp.) are distinctly more advanced floristically. Among them the tropical tribe Anthoboleae are the most primitive, having the ovary superior. The other tribes Osyrideae and Thesieae show advance in having the ovary inferior and are distinctly more subtropical and temperate in distribution. The large herbaceous semi-parasitic genus *Thesium* is widespread.

The allied Loranthaceae (26 gen., 900 sp.) show further specialisation in the direction of parasitism but the more tropical tribe Loranthoideae remain, on the whole, more primitive than the Viscoideae. Similarly the Balanophoraceae are highly specialised holoparasites on roots.

The Santalales are a group which illustrate extremely well on the one hand differentiation (chiefly in the direction of parasitism) as a result of the influence of the "biota" or the organic environment, and, on the other hand, response to drier and colder conditions, the influence of the inorganic environment.

ARISTOLOCHIALES. This order also illustrates differentiation resulting from the influence of the biota (*a*) in the Aristolochiaceae (6 gen., 200 sp.) as climbing shrubs and herbs, and (*b*) in the Rafflesiaceae (7 gen., 25 sp.) and the Hydnoraceae (2 gen., 10 sp.) as highly modified parasites.

POLYGONALES. The Polygonaceae (34 gen., 800 sp.) have three subfamilies of which the Rumicoideae with their cyclic flowers are probably to be reckoned the most advanced. The whole family is chiefly north temperate in distribution but the few tropical and southern representatives are, on the whole, relatively primitive phylogenetically, e.g. *Coccoloba* which has 125 species in tropical and subtropical America.

CENTROSPERMAE. Pax's arrangement (in Engler and Prantl.) of the families in this large order is illustrated by the following diagram:

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                         Caryophyllaceae
Amarantaceae \                 |                 / Aizoaceae
              >——Phytolaccaceae———<
Chenopodiaceae /               |                 \ Nyctaginaceae
                          Portulacaceae
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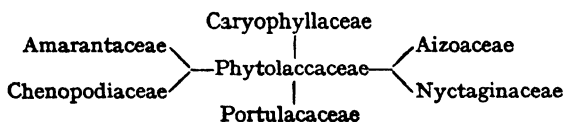
The central family Phytolaccaceae (24 gen., 120 sp.) are chiefly tropical or subtropical American and African trees, shrubs, or herbs. The Nyctaginaceae (20 gen., 170 sp.), which Hutchinson removes to the Thymelaeales, are also found in the warmer parts of both hemispheres but chiefly in America. They show some advance in the

direction of insect pollination, but in the tribe Pisoneae have inconspicuous flowers and straight embryos, an important character in this order where the embryo is usually curved. The Pisoneae are tropical or subtropical trees or shrubs and *Pisonia*, according to the fossil record, goes back to the Cretaceous.

All the other families show interesting and varied degrees of response to the process of climatic differentiation. The Amarantaceae (56 gen., 500 sp.) have three tribes of which the Celosieae, with two to many ovules, are distinctly the most tropical. The Amaranteae show advance in having the ovules reduced to one, and are more characteristic of dry, subtropical areas. They have produced a number of interesting endemic genera in the semi-desert regions of western South Africa. Others are very common subtropical weeds. The Gomphreneae are most advanced of all in having single ovules together with one-lobed anthers. They are subtropical and temperate in distribution and are still more common as weeds.

The Chenopodiaceae (75 gen., 500 sp.) are closely allied to the Amarantaceae and are mostly herbaceous halophytes distributed along the seashores of all the continents or in dry regions where the soil is rich in salts or as weeds.

The Aizoaceae (24 gen., 700 sp.) occur in the tropics of Africa, Asia, Australia, and South America, indicating their general tropical origin but they have become most highly differentiated in the drier subtropical regions particularly in South Africa. The Molluginoideae, with the perianth more or less divided and free from the superior ovary, are the most primitive and, at the same time, most mesophytic and tropical. The Ficoideae are a larger subfamily. The tribe Sesuvieae have the ovary superior and occur in the tropics or as seashore plants e.g. *Sesuvium* spp. The tribe Mesembryanthemeae with the ovary inferior are the most advanced especially in the large genus *Mesembryanthemum* with petaloid staminodes which includes over 500 species. [This genus has recently, however, been sub-divided by N. E. Brown.]

Not only floristically is the genus the most advanced in the family but ecologically in its many weird growth-forms it is, in many respects, one of the most highly specialised types of flowering plant. It is particularly characteristic of the dry Karroo region and desert areas of western South Africa, where the most highly evolved species occur. Species like *M. spinosum* are dominant over wide areas. In no family is the correlation between phylogenetic advance and increasing aridity better demonstrated.

The Portulacaceae (17 gen., 210 sp.) have one or two tropical or

subtropical forms, which are relatively primitive, e.g. *Talinella*, two species of Madagascar shrubs with the ovary bilocular instead of unilocular, but the majority are herbs, often annual, and the family, as a whole, is relatively recent and highly evolved. *Portulaca* has the ovary half inferior. The South African *Portulacaria*, a shrub often dominant in dry river valleys, has the ovules reduced to one.

The Caryophyllaceae (79 gen., 1500 sp.) are cosmopolitan but mostly temperate and chiefly herbaceous. The ovary is usually unilocular, owing to the breaking down of the septa between the carpels, but *Telephium*, which has species in Madagascar and the Mediterranean region, has the ovary incompletely trilocular with the ovules basal. The Silenoideae, with gamosepalous flowers are most advanced as regards pollination. They are largely Mediterranean but show wide extensions to other regions and particularly connections with the mountain ranges of the tropics and southern hemisphere. The whole family may be looked upon as a, possibly fairly early, response to temperate conditions in this (Centrospermae) circle of affinity.

RANALES. Whether the members of this order are, as many believe, the most primitive of all Angiosperms or not, there is no doubt that they are at least relatively primitive. The Magnoliaceae (13 gen., 110 sp.) are rich in supposed fossil representatives from the Cretaceous onwards, especially species of *Magnolia* and *Liriodendron*. Though at one time apparently very widespread they are at present confined to warmer regions, especially the south-east of North America and South-East Asia (see Good, 1925). Other large families, also mostly ancient, according to the fossil record, consist of tropical or subtropical or, rarely, warm temperate trees, shrubs, or woody lianes, viz. Menispermaceae (63 gen., 360 sp.), Anonaceae (76 gen., 900 sp.), Myristicaceae (16 gen., 250 sp.), Monimiaceae (30 gen., 250 sp.), Hernandiaceae (4 gen., 25 sp.) and most of the Lauraceae (48 gen., 1180 sp.). This great assemblage of about 250 genera and 3000 species of tropical and subtropical primitive woody plants is sufficiently impressive and by itself lends strong support to our view that the tropical flora is relatively ancient. Within this group of families there are also illustrations of the effects of the biota under tropical conditions in the production of numerous lianes, e.g. most of the Menispermaceae, while evolutionary advance with increasing aridity or lower temperatures is also shown, e.g. in the Lauraceae, the Perseoideae (anthers 4-locular) are more primitive than the Lauroideae (anthers 2-locular) which include *Laurus* and the parasitic genus *Cassytha*. Similarly the South African genera of the Menispermaceae,

Cissampelos and *Antizoma* are more advanced floristically than the tropical genera.

Among the more shrubby or herbaceous Ranales, which Hutchinson separates from the Magnoliales at the base of his scheme of phylogenetic classification, there are families, which are generally regarded as derivative and are certainly more temperate in distribution. The Berberidaceae (9 gen., 150 sp.) are chiefly north temperate and show advance in having a definite often trimerous arrangement of parts with the carpels generally reduced to one. They are shrubs or herbs. The Ranunculaceae (32 gen., 1200 sp.) are also usually herbaceous and temperate in distribution though the rather primitive genus *Clematis* is shrubby or climbing and more tropical or subtropical on the whole. Many of the Ranunculaceae are hygrophilous or aquatic. The two families Nymphaeaceae (8 gen., 60 sp.) and Ceratophyllaceae (1 gen., 3 sp.) are entirely aquatic and therefore to be considered derivative. The fact that the former goes back to the Cretaceous shows that the response of the Angiosperms to a purely aquatic environment began very early.

RHOEADALES. This order is, on the whole, more temperate in distribution and shows advance as compared with the Ranales in the cyclic arrangement of the parts of the flower, in syncarpy, etc. The Capparidaceae (43 gen., 450 sp.) are relatively primitive and consist mainly of tropical trees, shrubs or herbs and sometimes climbers. The majority, however, are adapted to rather dry conditions in the tropics and subtropics. The tribe Cleomoideae show transitions to the Cruciferae, a more specialised family (232 gen., 1900 sp.) which are mostly Mediterranean or north temperate in distribution. The Resedaceae (6 gen., 70 sp.) are a small derivative family of mainly Mediterranean xerophytic herbs and undershrubs. The Papaveraceae (30 gen., 600 sp.) are not so closely allied to the Capparidaceae and floristically in some respects are relatively primitive, though they are more specialised in others. They are mostly north temperate in distribution.

SARRACENIALES. In this order Engler includes the Sarraceniaceae (3 gen., 9 sp.), Nepenthaceae (1 gen., 60 sp.) and the Droseraceae (4 gen., 85 sp.) which all illustrate the interesting and well-known highly specialised response to the effect of the biota in their insectivorous habit, a sideline evolutionary experiment.

ROSALES. Most authorities connect the Rosales more or less closely with the Ranales. The Rosaceae (102 gen., 1700 sp.) are admittedly a somewhat heterogeneous family. The tropical subfamily,

the Chrysobalanoideae, though they have retained the woody character, have responded to the influence of their tropical living environment in the zygomorphy of their flowers. The rest of the Rosaceae are mainly temperate or mountain forms. The transition from the woody to the herbaceous type has in some cases e.g. *Alchemilla* been accompanied by marked reduction in their flowers.

Leguminosae (550 gen., 12,000 sp.). The evolutionary history of this great family (cf. Andrews, 1914) in all its numerous details illustrates extraordinarily well the differentiation of primitive tropical forms to suit nearly every kind of modern environment. The relatively primitive Mimosoideae and Caesalpinioideae are mainly tropical but show varied responses to increasing aridity. The more advanced Papilionatae are more temperate, though within this subfamily it is interesting to note that the relatively primitive tribe Sophoreae with the stamens free are still mainly tropical forms from which the more mountain and temperate Podalyrieae may have been derived. There are also a few tropical trees among the Papilionatae, e.g. *Millettia* and numbers of woody lianes, e.g. *Dalbergia*. The Connaraceae (20 gen., 250 sp.) are closely allied and are mostly climbers illustrating again differentiation in response to the biota.

Among the other families of the Rosales the same kind of differentiation is well illustrated. Thus the Pittosporaceae (9 gen., 110 sp.) and the Cunoniaceae (21 gen., 130 sp.) are mostly southern tropical-subtropical families of trees and shrubs, often climbing. The Hamamelidaceae (20 gen., 50 sp.) have an ancient fossil record going back to the Cretaceous and were at one time widespread but are now more restricted in distribution in subtropical and warm temperate regions (Asia, North America and South Africa). The small derivative family Myrothamnaceae (2 sp.) are xerophytic South African shrubs. Similarly the Brunelliaceae (10 sp.) in South America, the monotypic Eucommiaceae in China, the Bruniaceae (12 gen, 55 sp.) heath-like plants in the south-western region of South Africa, are all interesting endemic and probably derivative forms. In another direction the aquatic families Podostemonaceae (27 gen., 120 sp.), Tristichaceae (3 gen., 6 sp.) and Hydrostachyaceae (1 gen., 15 sp.) are highly modified derivative types, illustrating very well, as Willis has shown, the amount of differentiation that is possible under a relatively uniform environment.

The Saxifragaceae (78 gen., 700 sp.) are allied to the woody tropical Cunoniaceae, but show advance in being shrubby or herbaceous and in the prevalent sinking of the ovary. They are most

developed in temperate regions. The Crassulaceae (16 gen., 550 sp.) are in turn allied to the Saxifragaceae. They show response to increasing aridity particularly in South Africa. Within the limits of the large genus *Crassula*, according to Schönland's researches, the relatively mesophytic sections, e.g. *Tillaea* are more primitive floristically than the more xerophytic sections, e.g. *Globulea*.

GERANIALES. In this order a number of tropical woody families, Malpighiaceae (65 gen., 650 sp.), Trigoniaceae (3 gen., 30 sp.), Vochysiaceae (5 gen., 100 sp.), Dichapetalaceae (3 gen., 100 sp.) are tropical woody plants, often climbing. The Erythroxylaceae are a small family of tropical trees (2 gen., 200 sp.) which are allied to the more advanced, more herbaceous and more temperate family Linaceae (9 gen., 150 sp.). Similarly within the limits of the Oxalidaceae (7 gen., 300 sp.) tropical tree forms, e.g. *Averrhoa*, with the fruit a berry, lead on to shrubs, undershrubs and herbs, e.g. *Biophytum* (25 sp.) and the widely dispersed large genus *Oxalis* which has small temperate herbaceous species like the wood sorrel, *Oxalis acetosella*. None of the smaller families illustrate better the normal course of differentiation which, however, is similar to that within the larger families or within several allied families, where the details are sometimes more confusing. The Geraniaceae (11 gen., 500 sp.) are mostly temperate or mountainous in distribution and relatively advanced floristically. Some genera show marked response to increasing aridity in the drier subtropical regions as well, e.g. many species of the large genus *Pelargonium* in South Africa as well as *Sarcocaulon*. The Zygophyllaceae (28 gen., 160 sp.) are another relatively advanced family, including a large number of very xerophytic desert or semi-desert forms.

RUTALES. The Meliaceae (49 gen., 750 sp.), Simarubaceae (30 gen., 150 sp.) and the Burseraceae (13 gen., 400 sp.) are all relatively primitive, tropical, woody families. In the Burseraceae the genus *Commiphora*, which extends into the drier subtropics has the receptacle concave instead of convex, relatively an advanced type. The Rutaceae (125 gen., 950 sp.) include some relatively primitive tropical tree forms but also large numbers of more advanced, warm temperate shrubs, e.g. in the south-western regions of South Africa and in the Mediterranean region, both important regions in connection with the early beginnings of the temperate flora. The Australian temperate genus *Correa* is interesting, because it has developed sympetaly, giving an indication of a possible starting-point (among forms like the Rutaceae) for the Ericaceae. Hutchinson, however,

derives the Ericales from the Theales. The Polygalaceae (11 gen., 700 sp.) are an anomalous family of uncertain affinities included by Engler in the Geraniales, by Rendle (1925) in the Sapindales, by Hutchinson near the "Violales," close to the end of the series beginning with the Rhoeadales. The tropical forms are again the older. The tree genus *Xanthophyllum* is rather isolated but in the tribe Polygaleae the tropical genera *Carpolobia* and *Atroxima* have the petals unappendaged and well developed with the ovary 2- or 3-locular, while the large widespread genus *Polygala* with nearly 500 species is of a more advanced floristic type. The species of the tropical genus *Securidaca* are mostly lianes. The tropical genus *Epirrhizanthes* is holosaprophytic.

TRICOCCAE. The chief family of this order which Engler also includes in the Geraniales is the Euphorbiaceae (270 gen., 4500 sp.). The Buxaceae (7 gen., 60 sp.) are separated by Engler on the characters of the ovules and fruit and the Callitrichaceae (*Callitriche*, 26 sp.) are a small derivative, mainly aquatic, family.

The Euphorbiaceae, like the Leguminosae and other large families, illustrate once more extremely well the process of evolutionary differentiation from primitive tropical forms, towards more advanced types adapted to drier or colder conditions. In the section Platylobieae, the Phyllanthoideae (ovules 2 per loculus) are a more primitive group than the Crotonoideae (ovules 1 per loculus). In the former, the entirely tropical Daphniphylleae, with a very short embryo, are the most primitive of all. The slightly more advanced Brideliae are still mostly tropical while the still more advanced Phyllantheae are more highly differentiated. Within the limits of the single genus *Phyllanthus*, with over 400 species, are included trees, shrubs, undershrubs and herbs, many subtropical or adapted to grassland conditions and drier habitats. The Crotonoideae have eight tribes. In the tribe Crotoneae the genus *Croton* alone has 600 species of tropical or subtropical often rather xerophytic trees and shrubs in Africa, Asia and South America. The Jatropheae and Adraneae are tropical. The Cluyteae are more subtropical including shrubs and undershrubs adapted to grassland conditions. The Acalypheae are still more highly differentiated, including trees, climbers (*Dalechampia*, *Plukenetia*, etc.), grassland shrubs and herbs, cultivated and ruderal plants (*Ricinus*) and tender herbaceous plants of the forest undergrowth (*Seidelia*, *Leidesia*, *Micrococca*, *Adenocline*) as well as the temperate genus *Mercurialis*. Most advanced of all in the Platylobieae are the Euphorbieae, with their peculiar cyathium. Within the tribe, the

relatively primitive tropical West African genera *Anthostema* and *Dichostemma* have male flowers with a perianth. Closely allied to *Euphorbia* the West African genus *Elaeophorbia* has the fruit a drupe instead of a capsule. The genus *Euphorbia* with 750 species is in many ways one of the most highly evolved among the Angiosperms. In the moist tropics relatively mesophytic leafy species occur. In the drier subtropics, succulent and thorny species are typical and with reduction in size become extremely common (often dominant) in the semi-desert and desert regions of Africa. Finally the small herbaceous or annual species are the most highly evolved of all and have spread into the temperate regions of the northern hemisphere.

The other section of the family, the Stenolobieae, with narrow cotyledons represent a much earlier separation. They are all Australian except one monotype, *Dysopsis glechomoides*, in the Andes with a variety *hirsuta* in Juan Fernandez. Like so many of the early temperate groups, which apparently may have had a mountain origin, the Stenolobieae consist of heath-like forms with ericoid or pinoid leaves.

SAPINDALES and CELASTRALES. The Sapindaceae (130 gen., 1100 sp.) are the central and largest family of tropical trees and shrubs. Five genera and over 300 species are woody lianes. The Icacinaceae (48 gen., 200 sp.) are similar and also tropical. The Anacardiaceae (69 gen., 480 sp.) are more differentiated. The tribe Spondieae are relatively primitive in having 3–5 carpels, all with ovules, and are all tropical. The Rhoideae have only one fertile ovule and include the large genus *Rhus* which has spread into the drier subtropical and temperate regions. The tropical genus *Protorhus* is more primitive than either *Rhus* or *Heeria*, the latter a genus of xerophytic subtropical shrubs. The differentiation of the whole tribe from primitive, moist-tropical forms to desert and temperate forms is again most interesting.

The Celastraceae (51 gen., 500 sp.) are again tropical in origin, showing differentiation towards drier and colder conditions. Grouped round these tropical-subtropical woody families of the Sapindo-celastral series are a number of smaller families, the Hippocastanaceae (*Aesculus* and *Bellia*) north temperate and South American, Aceraceae (*Dipteronia* 2 sp. Central China and *Acer.*, 115 sp. north temperate), Stackhousiaceae (2 gen., 15 sp.) Australian and New Zealand, xerophytic herbs, Staphyleaceae (*Staphylea* 11 sp.) north temperate, the Balsaminaceae included here by Engler, with the large genus *Impatiens* (340 sp.) tropical and temperate, especially

in the mountains of India and Ceylon, Aquifoliaceae (4 gen., 280 sp.) widespread, the Coriariaceae (Coriaria 8 sp.) widespread, Empetraceae (3 gen., 4 sp.) north hemisphere and the Andes, Limnanthaceae (2 gen., 5 sp.) North American, all of which show to a greater or less extent advance with increasing response to climatic differentiation. There are also a few small and mainly tropical families, Hippocrateaceae (3 gen., 200 sp.) mostly climbing, Sabiaceae (3 gen., 70 sp.), Melianthaceae (3 gen., 30 sp.), Cyrillaceae (3 gen., 6 sp.), and Pentaphyllaceae (1 gen., 2 sp.). The Salvadoraceae (3 gen., 9 sp.) have sympetaly in *Salvadora*. They are African and Asiatic trees and shrubs.

RHAMNALES. Only two families are included in this order, the Rhamnaceae (50 gen., 500 sp.) and the Vitaceae (11 gen., 500 sp.). The Rhamnales show advance in their marked tendency to unisexuality by abortion and to perigyny or epigyny. The Rhamnaceae in the tropics and subtropics are generally adapted to drier conditions or more open situations and they extend into the temperate regions as well. The Vitaceae are either climbers or shrubs, many of the latter being very xerophytic and cactus-like.

MALVALES. In this order the Elaeocarpaceae (8 gen., 130 sp.) are tropical or subtropical trees or shrubs closely allied with the Tiliaceae (45 gen., 350 sp.) which are both tropical and temperate. The Bombacaceae (22 gen., 140 sp.) are entirely tropical, chiefly American, but include the African baobab (*Adansonia*), a prominent tree of drier regions. The Sterculiaceae (58 gen., 800 sp.) have many ancient tropical tree types but sharply contrasted with them are herbaceous genera showing floristic advance, e.g. *Hermannia* (200 sp.) adapted to open grassland conditions. The Malvaceae (50 gen. 1000 sp.) show floristic advance particularly in the Androecium. A few are moist tropical but the majority are drier subtropical or temperate shrubs or herbs.

PARIETALES. Here the Flacourtiaceae (84 gen., 640 sp.) the Turneraceae (7 gen., 100 sp.), Winteranaceae (4 gen., 8 sp.), Cochlospermaceae (3 gen., 20 sp.) and *Bixa orellana*, the only species of the Bixaceae, are predominantly tropical and subtropical woody plants. In the Flacourtiaceae many genera extend into the drier subtropics but Warburg (in Engler and Prantl) derives all the tribes from the Erythrospermeae which are tropical, another independent testimony in favour of our general theory.

Contrasted with the tropical group once more, a number of more advanced smaller, allied families have a temperate or mountain

distribution, the Cistaceae (7 gen., 140 sp.) north temperate shrubs and herbs, the Malesherbiaceae (1 gen., 25 sp.) herbs and undershrubs of western South America, the Loasaceae (13 gen., 230 sp.) mostly herbs, sometimes twining, of the Andes region.

The suborder Tamaricineae show advance in having exendospermic seeds or a little endosperm which is starchy. They include the Elatinaceae (2 gen., 35 sp.) herbs or water plants, Frankeniaceae (4 gen., 64 sp.) halophytes, and Tamaricaceae (4 gen., 90 sp.) also mostly halophytes, all specialised and derivative types.

The Passifloraceae (13 gen., 380 sp.) and the Achariaceae (3 gen., 3 sp.) show response to the biota in their climbing habit. They have rather advanced floral structure.

In the Peponiferae, the Cucurbitaceae (100 gen., 800 sp.) may come here. Engler places them among the Sympetalae. In any case, they are another advanced family, under the influence of the biota. Similarly the Begoniaceae (5 gen., 450 sp.) show the effects of competition for space. They are herbs of the forest undergrowth. The exact affinities of the family, however, are obscure. This applies also to the Violaceae (18 gen., 450 sp.) which are included here by Engler. Within the limits of this family, the tropical and subtropical woody Rinoreae, with regular flowers are more primitive and contrast strongly with the temperate herbaceous Violeae, which have irregular flowers.

The GUTTIFERALES, included by Engler in the Parietales, are largely tropical, and contain the Dilleniaceae (14 gen., 320 sp.), the Ochnaceae (22 gen., 250 sp.), the Guttiferae (50 gen., 850 sp.), the Dipterocarpaceae (19 gen., 340 sp.), the Theaceae (20 gen., 200 sp.), the Marcgraviaceae (5 gen., 50 sp.). Advance and differentiation, however, are again shown in the production of lianes and epiphytes (Marcgraviaceae), in shrubs adapted to drier conditions (Ochnaceae), in herbs which become widespread and temperate, e.g. *Hypericum* (Guttiferae).

OPUNTIALES. Cactaceae (23 gen., 1500 sp.). The affinities of this family of highly specialised succulents are quite uncertain. They are all American except *Rhipsalis cassytha*, which is often epiphytic or grows on rocks and is widely dispersed in the tropics of the old world.

MYRTIFLORAE. In this order union of the styles, sinking of the ovary, exendospermy and other features all show advance. None of the families are very primitive though Guppy looks on the prevalent vivipary of the Mangroves (some of the Rhizophoraceae) as a primitive character. The Rhizophoraceae (18 gen., 60 sp.), the Lecythi-

daceae (19 gen., 250 sp.) are families of tropical trees mostly hygrophilous. In the Combretaceae (17 gen., 450 sp.) the West African tropical Strephonematoideae are primitive in having the ovary only half inferior. The more advanced Combretoideae are characteristic of the drier regions. They also include climbers (e.g. *Quisqualis*). The Myrtaceae (76 gen., 3000 sp.), as in the case of the Leguminosae, Euphorbiaceae and several other large families, illustrate our general theory extremely well (cf. Andrews, 1913). The Myrtoideae are, on the whole, more tropical or more hygrophilous than the Leptospermoideae, which are distributed more over drier subtropical areas, especially the large genus *Eucalyptus* in Australia. Both subfamilies, however, show some degree of response to climatic differentiation. In the Leptospermoideae, the large genus *Eugenia* with over 600 sp. is widespread over the tropics and subtropics of both worlds and shows a range of forms from large trees down to slightly woody undershrubs. *Myrtus communis* is the only European representative.

In the large but very natural tropical and subtropical family, the Melastomaceae (170 gen., 2800 sp.), the range of forms includes trees, shrubs, climbers, epiphytes, herbs, marsh and aquatic plants, another interesting field for the study of differentiation.

As in the other cases, the more purely herbaceous families of the Myrtiflorae contrast with the woody families in being more temperate in distribution and more advanced floristically, e.g. the Onagraceae (39 gen., 500 sp.), chiefly north temperate, Halorrhagaceae (7 gen., 150 sp.) widespread marsh or aquatic plants and Hippuridaceae (*Hippuris vulgaris*) aquatic. The Lythraceae include some tree forms, tropical or subtropical, and derivative herbs often with reduced flowers, cosmopolitan or temperate.

The THYMELAEINEAE are included by Engler as a suborder of the Myrtiflorae. The Thymelaeaceae (41 gen., 450 sp.) are the central family, allied perhaps to the South African woody genus (*Olinia*, 7 sp.) of the Oliniaceae. Among the Thymelaeaceae the tropical West African genus of trees *Octolepis* is the most primitive, having a flat receptacle and the ovary 4–5-locular. The Aquilarioideae and Phaleroideae have the ovary bilocular and are spread over the Indo-Malayan region, China, Australia, the Philippines and tropical Africa. The most advanced subfamily is the Thymelaeoideae with the ovary unilocular and a much hollowed receptacle. They consist of shrubs, undershrubs, often heath-like, and herbs, distributed over the drier subtropical regions, especially South Africa, and in the genus *Daphne* reaching Europe.

Allied to the Thymelaeaceae and also often heathlike are the small south-western Cape families, Penaeaceae (5 gen., 35 sp.) and *Geissoloma* (Geissolomataceae) as well as the north temperate Eleagnaceae (3 gen., 35 sp.).

UMBELLIFLORAE. The Araliaceae (55 gen., 660 sp.) are chiefly tropical and subtropical trees and shrubs and they contrast with the more advanced and mostly herbaceous and temperate family, the Umbelliferae (270 gen., 2700 sp.). Such a pairing between large well-defined families illustrates extremely well the relationship between the tropical and temperate floras. The Cornaceae (10 gen., 100 sp.) are not so closely related to the Araliaceae but they do show floristic advance and are distributed over the temperate regions and mountains of the tropics. They possibly represent a rather ancient temperate type.

SUMMARY

1. Ecological differentiation among the Angiosperms is regarded as having taken place, first of all and for the longest period of time, under relatively unchanging moist tropical conditions. Such differentiation may be due to internal forces, and in so far as this is the case may be entirely independent of the external environment. Under favourable conditions, however, the living environment or biota is important.

2. The great lapse of time since the Angiosperms appeared, during which warm, moist, favourable conditions have prevailed in the tropical regions, has allowed of the differentiation of the great family groups and, under the influence of the biota, of the following main types of plant form, trees (evergreen, hard-wooded, sparingly branched, leathery-leaved, large-leaved), lianes (progressing from the woody to the herbaceous), epiphytes, mesophytic shrubs, undershrubs and herbs of the forest undergrowth and forest margins, as well as still more specialised forms, parasites, saprophytes, and insectivorous plants.

3. More recent climatic differentiation has been responsible for the production of types of plant form adapted to drier conditions, on the one hand, and colder conditions on the other. Some rather ancient temperate types appeared very early, apparently chiefly on mountain ranges, and in the southern hemisphere. The Mediterranean region is also an important centre for certain temperate groups. Since differentiation in response to increasing aridity and lower temperatures has been on the whole relatively recent, it follows that evidence in support of the view must be sought for in the narrower circles of

affinity, the more well-defined orders, the families and some of the larger genera.

4. Since any selected evidence must remain unconvincing, it is necessary to pass in review all the families of the Angiosperms; considerations of space have made it necessary to do so in a somewhat condensed form. Previous writers have done so in greater detail for some of the larger families and particularly Andrews for the Leguminosae and Myrtaceae. The main facts referred to in this paper are set forth in the form of a table in the following appendix.

APPENDIX

	Systematic position	Relatively primitive, tropical to subtropical, hygrophilous or mesophytic	Relatively advanced, more temperate or more xerophytic
1.	Fagales	Evergreen forms	Deciduous forms
2.	Urticales	Moraceae	Cannabinaceae
3.	Urticales	Moraceae	Urticaceae
4.	Ulmaceae	Celtidoideae	Ulmoideae
5.	Santalales	Olacaceae	Grubbiaceae
6.	Santalales	Olacaceae	Santalaceae
7.	Santalaceae	Anthoboleae	Osyrideae
8.	Santalaceae	Anthoboleae, Osyrideae	Thesieae
9.	Loranthaceae	Loranthoideae	Viscoideae
10.	Polygonaceae	Coccoloboideae	Rumicoideae
11.	Centrospermae	Phytolaccaceae Nyctaginaceae	Amarantaceae Chenopodiaceae Aizoaceae Portulacaceae Caryophyllaceae
12.	Amarantaceae	Celosieae	Amaranteae Gomphrenoideae
13.	Aizoaceae	Molluginoideae	Ficoideae
14.	Ficoideae	Sesuvieae, Aizoeae	Mesembrianthemeae
15.	Aizoaceae	Other genera	*Mesembrianthemum*
16.	Portulacaceae	Other genera	*Portulaca, Portulacaria*
17.	Ranales	Magnoliaceae Anonaceae, Menispermaceae Myristicaceae, Monimiaceae Lauraceae	Berberidaceae Ranunculaceae Nymphaeaceae Ceratophyllaceae
18.	Menispermaceae	Other genera	*Cissampelos, Antizoma*
19.	Lauraceae	Perseoideae	Lauroideae
20.	Ranunculaceae	*Clematis*	Other genera
21.	Archichlamydeae	Ranales	Rhoeadales
22.	Rhoeadales	Capparidaceae	Cruciferae Resedaceae
23.	Capparidaceae	Capparidoideae	Cleomoideae
24.	Rosaceae	Woody genera	Herbaceous genera
25.	Leguminosae	Mimoseae Caesalpinoideae	Papilionatae
26.	Papilionatae	Sophoreae	Other tribes
27.	Rosales	Pittosporaceae Cunoniaceae Hamamelidaceae	Myrothamnaceae Brunelliaceae, Bruniaceae Saxifragaceae, Crassulaceae
28.	*Crassula*	*Tillaea* sect.	*Globulea* sect.

	Systematic position	Relatively primitive, tropical to subtropical, hygrophilous or mesophytic	Relatively advanced, more temperate or more xerophytic
29.	Geraniales	Malpighiaceae, Erythroxylaceae	Linaceae, Oxalidaceae, Geraniaceae, Zygophyllaceae
30.	Erythroxylaceae	*Aneulophus*	*Erythroxylon*
31.	Oxalidaceae	*Averrhoa*	*Oxalis*
32.	Rutales	Meliaceae, Burseraceae, Simarubaceae	Rutaceae
33.	Burseraceae	Tropical genera	*Commiphora*
34.	Rutaceae	Tropical trees	Mountain and temperate shrubs
35.	Polygalaceae	*Carpolobia, Atroxima*	*Polygala*
36.	Euphorbiaceae	Platylobieae	Stenolobieae
37.	Platylobieae	Phyllanthoideae	Crotonoideae
38.	Phyllanthoideae	Daphniphylleae	Other tribes
39.	Phyllanthoideae	Bridelieae	Phyllantheae
40.	Crotonoideae	Crotoneae, Jatropheae, Adreneae	Cluytieae
41.	Crotonoideae	Crotoneae, Jatropheae, Adreneae	Acalypheae
42.	Euphorbiaceae	All other tribes	Euphorbieae
43.	Euphorbieae	*Anthostema*, *Dichostemma*	*Euphorbia*
44.	*Euphorbia*	Tropical species	Desert and temperate species
45.	*Euphorbia*	Perennials	Annuals
46.	Sapindales, Celastrales	Icacinaceae, Sapindaceae	Anacardiaceae, Celastraceae
47.	Anacardiaceae	Spondieae	Rhoideae
48.	Sapindales, Celastrales	Icacinaceae, Sapindaceae, Celastraceae	Aceraceae, Hippocastanaceae, Aquifoliaceae
49.	Sapindales, Celastrales	Icacinaceae, Sapindaceae, Celastraceae	Stackhousiaceae, Staphylaceae
50.	Sapindales, Celastrales	Icacinaceae, Sapindaceae, Celastraceae	Coriariaceae, Empetraceae, Limnanthaceae
51.	Archichlamydeae	Sapindales, Celastrales, Geraniales	Rhamnales
52.	Malvales	Elaeocarpaceae	Tiliaceae
53.	Malvales	Sterculiaceae	Malvaceae
54.	Sterculiaceae	Tropical trees	*Hermannia*
55.	Parietales	Flacourtiaceae, Turneraceae, Winteranaceae, Bixaceae	Cistaceae, Malesherbiaceae, Loasaceae
56.	Parietales	Flacourtiaceae, Turneraceae, Winteranaceae, Bixaceae	Elatinaceae, Frankeniaceae, Tamaricaceae
57.	Flacourtiaceae	Erythrospermeae	Other tribes
58.	Violaceae	Rinoreae	Violeae
59.	Guttiferales	Tropical genera	*Ochna, Hypericum*
60.	Myrtiflorae	Rhizophoraceae, Lecythidaceae	Combretaceae
61.	Combretaceae	Strephonematoideae	Combretoideae
62.	Myrtaceae	Myrtoideae	Leptospermoideae
63.	*Eugenia*	Tree forms	Undershrubs

	Systematic position	Relatively primitive, tropical to subtropical, hygrophilous or mesophytic	Relatively advanced, more temperate or more xerophytic
64.	Myrtiflorae	Myrtaceae Melastomaceae	Onagraceae Halorrhagaceae
65.	Lythraceae	Tree forms	Herbaceous forms
66.	Thymelaeaceae	*Octolepis*	All other genera
67.	Thymelaeaceae	Aquilarioideae Phaleroideae	Thymelaeoideae
68.	Thymelaeineae	Thymelaeaceae	Penaeaceae Geissolomataceae Eleagnaceae
69.	Umbelliflorae	Araliaceae	Umbelliferae
70.	Umbelliflorae	Araliaceae	Cornaceae

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CHAPTER III

SYMPETALAE AND MONOCOTYLEDONS

SYMPETALAE (3550 gen., 50,500 sp.)

THE Sympetalae, as a whole, are undoubtedly more advanced than the Archichlamydeae, but if, as is now generally the accepted belief among botanists, the former are polyphyletic in origin, it may very well be that certain groups developed much sooner than others. Further, as a result of the continued process of differentiation in all the orders of the dicotyledons, certain families among the Archichlamydeae may be more recent and more advanced than some families among the Sympetalae. The Sympetalae are not without representation as far back as the Cretaceous, and several families of the Archichlamydeae have almost certainly been evolved since then. Yet, in a general way, the Sympetalae show their high development in being predominantly herbaceous and, on the whole, extensively adapted to modern conditions, either outside the tropics or within the tropics in the drier regions or in open grassland habitats. In the moist tropical forest habitats, they are relatively less abundant. Tree forms are comparatively rare among them. In so far as they are represented in tropical forest, they show the effects of the biota, and consist largely of climbing forms or herbaceous undergrowth.

Nevertheless, within each circle of affinity, they continue to illustrate extremely well the general principles set forth in chapter II. Since the relationships of the families are better understood, on the whole the story of their evolution is clearer than it is among the Archichlamydeae.

ERICALES. This relatively primitive order includes the Ericaceae (77 gen., 1550 sp.), the Epacridaceae (23 gen., 340 sp.), the Pirolaceae (10 gen., 30 sp.), the Diapensiaceae (6 gen., 9 sp.) and the Clethraceae (*Clethra* 30 sp.) with the degenerate family of root parasites, the Lennoaceae (3 gen., 5 sp.). The great central and most widely distributed family is the Ericaceae, of which, species of *Andromeda* are said to go back to the Cretaceous. They may possibly be connected with the Geraniales or Rutales. The shrubby Rutaceae, with their occasional sympetaly (as in the tribe Cusparieae), afford us a hint of a possible starting-point for the Ericaceae. As we have seen, the

shrubby Rutaceae are, at the present time, mostly mountainous or warm temperate in distribution while the tree forms of the same family, which are floristically more primitive, are more tropical. The Ericaceae themselves are not all sympetalous. The small tribe Ledeae with four genera in North and South America, and one in Japan, are polypetalous. The chief centre of the tribe Rhododendreae is the mountainous region of South-East Asia from South China to the Himalayas. The small tribe Phyllodoceae are mostly North American and circumpolar. All these belong to the subfamily Rhododendroideae, an ancient mountain and temperate type. The subfamily Arbutoideae may be even more ancient. The tribe Andromedeae are mostly North American, but include one genus from the mountains of South-East Asia and one (*Agauria*), with seven species, on the mountains of tropical Africa; the tribe, Gaultherieae is very widely distributed, having *Gaultheria* in America, Japan, the Himalayas and Tasmania, and four other genera (India, Malaya, Tasmania, New Zealand, South-East Australia, North and Central America); the tribe Arbuteae include *Arbutus* (Mediterranean region, Western Asia and North America), *Arctostaphylos* (north temperate and arctic) and *Arctous*, circumpolar. The subfamily Vaccinioideae (which, according to Wernham may have had a distinct origin, possibly from the Rosales) include 20 genera, chiefly from the Himalayas, and various tropical mountains in South America. The genus *Vaccinium* itself is mainly north temperate, but occurs in the Andes and in the mountains of Madagascar. Finally the subfamily Ericoideae are particularly characteristic of the mountainous south-western region of the Cape where *Erica* alone has 480 species, and there are many smaller genera. The Ericoideae extend along the African mountain ranges to Europe; *Erica arborea* on the tropical African mountains and in the Mediterranean may represent a rather ancient type.

The distribution of the Ericaceae, as a whole, would indicate that they represent another ancient, temperate type, which probably originated on the mountain ranges of the world. Among the Archichlamydeae, families like the Proteaceae, Grubbiaceae, Bruniaceae, Penaeaceae, Geraniaceae, the shrubby Rutaceae, Empetraceae and others have probably had a similar origin. The fact that the Epacridaceae, which differ from the Ericaceae chiefly in the isomery of the stamens, have almost entirely taken the places of the latter in Australia, is significant. It would seem to point to a separation of the two families since the connections of Australia and the other

continents were broken. The Epacridaceae do, however, have a few representatives outside Australia (in India, New Zealand, Hawaii and South America). All the families of the Ericales, however ancient they may be, are to be considered derivative; and if they are to be connected, as is generally believed, with the Rutales, then their ancestors were again more tropical, but the detailed lines of origin are no longer very obvious. The tropical origin and differentiation of the Geraniales and Rutales have already been dealt with.

PRIMULALES. In this order, the relatively tropical or subtropical Myrsinaceae (32 gen., 1000 sp.), a family of trees and shrubs, contrasts with the more advanced and more temperate Primulaceae (28 gen., 250 sp.), a family of herbs. Among the Myrsinaceae, the petals are free in *Embelia* which has about sixty species in the tropics of Asia and Africa. The more subtropical or more xerophytic genus, *Maesa*, on the other hand, shows advance in having the ovary inferior or half inferior. The small tropical family, Theophrastaceae (4 gen., 70 sp.), are allied to the Myrsinaceae. The Plumbaginaceae, (10 gen., 280 sp.), though allied to the Primulales, are not so closely connected. They show advance in the reduction of the ovules to one and are commonest in halophilous habitats.

The EBENALES are the third order of the Pentacyclidae (which also include the Ericales and Primulales). The Ebenales are almost entirely tropical or subtropical trees, including the Sapotaceae (50 gen., 650 sp.), Ebenaceae (5 gen., 320 sp.), Styracaceae (8 gen., 120 sp.) and Symplocaceae (*Symplocos* 300 sp.). The order is generally considered to have had two distinct lines of development, one represented by the Sapotaceae and the other by the remaining families. In the Sapotaceae, rather more advanced genera, e.g. *Mimusops* and *Sideroxylon*, extend outside the tropics particularly along seashore habitats.

Similarly in the Ebenaceae, genera like *Royena* and *Euclea* have many species adapted to drier subtropical conditions and are, on the whole, more advanced than the more tropical genera *Diospyros* and *Maba*.

The CONTORTAE. In this order the Oleaceae (25 gen., 420 sp.) are somewhat isolated. They show advance in having the ovules reduced to 2 or 1 per loculus, and the stamens reduced to two and are mostly drier subtropical or warm temperate in distribution. The Ash (*Fraxinus excelsior*) with its reduced polygamous flowers is a native of Britain. The other families, Loganiaceae (33 gen., 550 sp.), Apocynaceae (165 gen., 1300 sp.), Asclepiadaceae (267 gen., 2200 sp.) and

Gentianaceae (71 gen., 900 sp.) come closer together, and all illustrate our general principles of ecological differentiation extremely well.

The Loganiaceae are floristically the most primitive, and are mostly tropical or subtropical with a few warm temperate representatives. The subfamily Loganioideae are more primitive and more tropical than the Buddleioideae. The Apocynaceae are more advanced and within the tropics show the effects of the biota in their prevalent climbing habit. Some are shrubs adapted to somewhat drier subtropical conditions, and one or two, e.g. *Vinca* spp., have penetrated into temperate regions. The higher Apocynaceae connect with the Asclepiadaceae, the Periplocoideae being a transitional tribe with loose pollen grains. The Asclepiadaceae under forest conditions are mostly climbers which become increasingly xerophytic in the drier types of subtropical savannah-forest and scrub. The climbing habit is retained by several distinct tribes, ecological evolution, as often happens, thus cutting across floristic evolution. Many very large genera of the family have adopted a geophytic habit under grassland conditions. Some species have penetrated into temperate regions. A few are common weeds. The most highly specialised of all, floristically and otherwise, are the desert or semi-desert forms, particularly the tribe Stapelieae so characteristic of the drier parts of South Africa.

The Gentianaceae have not developed in such a specialised direction in response to insect visits, but they are, nevertheless, more advanced than the others in having the ovary usually unilocular and in their prevalent herbaceous habit. A few are shrubs, but the great majority are herbs. They occur all over the world and have become differentiated to suit all kinds of habitats. They include forest and grassland herbs, temperate region plants, arctic and alpine plants, halophytes, saprophytes (*Voyria*), marsh plants and water plants (*Limnanthemum*).

TUBIFLORAE. The Polemoniaceae (13 gen., 280 sp.) are a rather isolated small family, chiefly North American, but represented also in South America, Europe and Asia. They usually have three carpels, and it is difficult to say what their history or exact relationships have been.

The Convolvulaceae (45 gen., 1150 sp.) have the flowers usually large and not crowded into dense inflorescences, and probably represent the modern development of the stock (not very distinct from that of the Contortae) that gave rise to all the other families of the Tubiflorae. The tropical forms include a few small trees, many

shrubs and climbers as well as herbs; in temperate regions herbaceous forms are commoner, including annuals. One widespread genus *Cuscuta* has become parasitic.

From the original stock, two other small families have probably evolved directly—the Hydrophyllaceae (17 gen., 180 sp.), a family of herbs and undershrubs, chiefly North American with a few in South America, Asia and Africa, and also the Nolanaceae (3 gen., 50 sp.) on the west coast of South America.

There remain two great diverging lines, leading to the Personales on the one hand and the Lamiales on the other, if we adopt Bentham and Hooker's names. The Solanaceae (83 gen., 2100 sp.) come somewhere near the ancestral forms of the Personales. They consist of trees, shrubs and herbs with their main centre of distribution in Central and South America, extending into the temperate regions. The tropical tribes, Cestreae and Salpiglossideae, with the embryos straight or only slightly curved are relatively primitive in some respects, but the Salpiglossideae once more illustrate the effects of the biota, and in the more superficial flower characters show advance in the reduction of the stamens to four or two. Zygomorphy in the flowers, as we have seen, may occasionally develop in tropical representatives to a greater extent than in temperate, but, as a rule it is confined to subordinate and derivative types of plant form. The Bignoniaceae (109 gen., 670 sp.) are also a rather primitive member of the Personales. They are a family of trees and shrubs, often climbing, tropical and subtropical in distribution, mostly in Brazil. One genus *Catalpa* is common to the Old and New Worlds. The Bignoniaceae show interesting responses to drier subtropical conditions e.g. in the South African genus *Rhigozum*. The small families Pedaliaceae (17 gen., 70 sp.) and Martyniaceae (3 gen., 10 sp.) of seashore or desert or ruderal plants are allied to the Bignoniaceae, but distinctly derivative and more advanced.

The Scrophulariaceae (210 gen., 3000 sp.) connect with the Solanaceae, through the tribe Verbasceae. Ecologically they show a large amount of interesting differentiation. There are a few tropical or subtropical tree forms (e.g. *Paulownia, Halleria*), several shrubby genera adapted to drier subtropical conditions (e.g. *Bowkeria*), several climbers (e.g. *Maurandia, Rhodochiton*), an epiphytic genus (*Dermatobotrys*), marsh and aquatic forms (e.g. *Limosella, Diclis*), a large number of hemiparasitic genera (e.g. *Euphrasia, Bartsia, Pedicularis, Cycnium, Melasma, Striga*), a number of holo-parasites (e.g. *Harveya, Hyobanche*) and a great many subtropical and temperate

herbs. In allied small families the process of differentiation is carried still further. There is reduction of the ovules in the Selaginaceae (often included as a tribe of the Scrophulariaceae). The Globulariaceae (3 gen., 20 sp.) have the ovary unilocular with one ovule. The Orobanchaceae (12 gen., 140 sp.) are parasites chiefly north temperate in distribution. The Lentibulariaceae (6 gen., 260 sp.) are marsh or water plants usually insectivorous. The Gesneraceae (97 gen., 1150 sp.) are a larger allied family which show a tendency to epigyny. They include some woody plants but are mostly herbaceous and are often rather common as undergrowth in tropical and subtropical forest.

The Acanthaceae (214 gen., 2400 sp.) are also particularly characteristic of the forest margins and forest undergrowth in tropical and subtropical regions representing a highly specialised response to the effects of the biota. It is again interesting to note that the more primitive subfamilies, Nelsonioideae, Mendonsioideae and Thunbergioideae, are distinctly more tropical than the Acanthoideae many members of which are adapted to grassland conditions in subtropical regions, and some extend into temperate regions, e.g. in the Mediterranean countries, North America, Australia and South Africa.

The small family Myoporaceae (5 gen., 90 sp.) found chiefly in Australia and the neighbouring islands are placed by Engler near the Acanthaceae but Bentham and Hooker included them in the Lamiales.

The Boraginaceae (97 gen., 1500 sp.) come nearest to the ancestral stock of the Lamiales, as the Solanaceae do in the case of the Personales. The Boraginaceae illustrate very well the same lines of differentiation. The floristically primitive tribes, with their styles inserted at the apex of the ovary, and their fruits drupaceous, are all, more or less, tropical or subtropical and woody including the Cordioideae (3 gen. of which *Cordia* is the largest with 230 sp.), the Ehretioideae (10 genera) and the Heliotropoideae (3 gen. of which *Tournefortia* has 120 sp. and *Heliotropium* 220 sp.). The more advanced herbaceous Boraginoideae, on the other hand, with their gynobasic styles and schizocarpic fruits, are chiefly temperate. The Mediterranean region is an important centre of their distribution. The Labiatae (170 gen., 3400 sp.) show advance in their zygomorphy and efficient protection of fruit and seed by the persistent calyx, etc. Like the Acanthaceae, they are rather prominent as forest margin plants in subtropical regions, but they have become more widespread and differentiated in temperate regions. The majority are under shrubs and herbs often showing a certain degree of xerophytism,

particularly in the prevalent production of ethereal oils. The Mediterranean region is again one of their most important centres. The Verbenaceae (80 gen., 900 sp.) represent a sideline development from the Lamial stock. Several have remained rather primitive with straight or half-inverted ovules, e.g. *Avicennia*, one of the tropical Mangroves. The warm temperate mountain representatives at the Cape show advance in having basal inverted ovules, but have retained endospermous seeds and in several genera have more or less regular flowers, i.e. they show advance in some respects but not in others. We have already noted many features of this mountain flora which indicate that it represents rather an ancient temperate type. As in the case of many other families (Penaeaceae, Grubbiaceae, Bruniaceae, Leguminosae, Thymelaeaceae, etc.), the Verbenaceae in mountainous regions such as South Africa have produced ericoid forms (e.g. *Stilbe*, *Euthystachys*, *Eurylobium*, etc.).

The Plantaginales (Plantaginaceae) have three genera, viz. *Bougueria* (1 sp. in Andes), *Litorella* (1 sp. in South America, and 1 in Europe) and *Plantago* (200 sp. cosmopolitan, but chiefly temperate). The affinities of the family are uncertain. They probably represent degraded forms allied to the Tubiflorae.

INFERAE. The epigynous Sympetalae are considered to be the highest evolved group of flowering plants. Though the number of families included are few, the number of species is about 22,000 or not much less than one half of all the Sympetalae.

Engler (following Eichler) includes the Cucurbitaceae (97 gen., 750 sp.) among the Inferae, though they have also been placed near the Passifloraceae or near the Loasaceae and Begoniaceae among the Archichlamydeae. Whatever their exact affinities, there is no doubt that they are a rather highly evolved family, consisting of herbs, chiefly climbing and annual, found in the warmer regions of the world, and once more in their derivative character showing the influence of the biota. Engler divides the other Inferae into the Rubiales and Campanulatae, the latter including the Compositae, which are considered to be connected with the Campanulaceae. Bentham and Hooker and other writers have connected the Compositae more closely with the Dipsaceae (included by Engler in the Rubiales).

RUBIALES. In this order the Rubiaceae (400 gen., 5000 sp.) are relatively primitive. Of the two subfamilies, the Cinchonoideae, with two or more ovules in each loculus, are more primitive and distinctly more tropical than the Coffeoideae which have only one ovule in each

loculus. Both subfamilies are mainly woody and, at the same time, both have produced some herbaceous genera adapted to drier or colder conditions, e.g. *Oldenlandia* among the Cinchonoideae and *Galopina, Anthospermum, Spermacoce, Hydrophylax, Richardsonia* and the tribe Galieae among the Coffeoideae. The Galieae are a rather advanced tribe adapted to temperate conditions. The whole family again illustrates very well the general lines of ecological differentiation among the Angiosperms, the moist tropical forms primitive, the drier subtropical forms and the temperate forms all derivative and more advanced.

The Caprifoliaceae (11 gen., 350 sp.) are mainly north temperate with a few representatives on tropical mountains. They show advance in the marked tendency towards zygomorphy (e.g. in *Lonicera* with 100 sp. or more than one-fourth of the whole, as well as in others), in the oligomery of the androecium, as seen in *Dipelta* and *Linnaea*, and in a slight tendency towards aggregation of the flowers.

The Adoxaceae include only *Adoxa moschatellina* which is widespread over the north temperate zone. It shows advance in all its features, being a low herb, with compound leaves, and underground storage in a creeping rhizome. Its flowers are aggregated into globular heads with the terminal flowers usually tetramerous, the others pentamerous.

The Valerianaceae (10 gen., 350 sp.) are temperate or mountainous in their distribution, and consist of herbs with asymmetrical flowers aggregated in cymose panicles. The corolla is often spurred at the base, and the calyx often forms a pappus after flowering as in the Compositae. The stamens are from one to four, epipetalous, and there is only one ovule. Some are annuals, but the majority are perennials with underground rhizomes. All those features show advance. The Dipsaceae (10 gen., 160 sp.) are also temperate and mountainous in distribution, with the Mediterranean region as one of their main centres. They again show advance in being herbaceous, with the flowers aggregated, and showing zygomorphy and division of labour, and in having the ovules reduced to one. The calyx again plays a part in seed dispersal.

Not only then does the differentiation of the central and most primitive family of the Rubiales, the Rubiaceae, illustrate our general principles extremely well, but the differentiation of the order Rubiales, as a whole, shows how the same principles apply on a larger scale, and within a wider circle of affinity. The relatively advanced characters of all the temperate families are very striking.

CAMPANULATAE. The vast majority of the plants belonging to this order are herbaceous and they are all, more or less, of an advanced type floristically. The Campanulaceae (65 gen., 1500 sp.) are the most heterogeneous of the families having the ovary not always quite inferior, and the petals not always quite united. The ovary is usually multilocular and multiovulate, but there is a marked tendency towards a bicarpellary condition which rarely becomes unilocular (e.g. in *Merciera*). The anthers may be free, but they tend towards union in the Lobelioideae, where the corolla is zygomorphic. There is a tendency also towards aggregation of the flowers in some, e.g. *Jasione* and *Phyteuma*. In a word, the Campanulaceae show the beginnings of various lines of advance, which have reached their culmination in the Compositae, and were also seen, to some extent, in the Valerianaceae and Dipsaceae. As in the case of these families the distribution of the Campanulaceae is in the main temperate or mountainous. The tree Lobelias of the African mountains reach a height of 15 ft. and are a very interesting type of plant form. There are a few, small herbaceous families among the Campanulatae: the Goodeniaceae (11 gen., 300 sp.) chiefly Australian, the Brunoniaceae (*Brunonia*) Australia and Tasmania, the Stylidiaceae (6 gen., 120 sp.) Australia, South America and Asia, and the Calyceraceae (4 gen., 25 sp.) South America, each of which illustrates certain rather specialised and minor lines of development, which it is unnecessary for our present purpose to describe in detail.

The Compositae (950 gen., 13,500 sp.). All authorities are agreed that the Compositae are the most highly evolved and successful of all plants, and best adapted to modern environmental conditions. While they are quite cosmopolitan in their distribution, they are relatively rather scarce in the moist tropical regions and except for a few climbing species are hardly represented in tropical rain forest. They are, on the other hand, abundant in the drier subtropical and temperate regions. They are very common on tropical mountain ranges where woody types are characteristic, including tree Senecios and many shrubby forms, cushion forms, etc. There are a few tree forms adapted to drier subtropical or psammophilous habitats, e.g. *Tarchonanthus*, *Brachylaena*. But the vast majority are undershrubs or herbs. In grassland areas with increasing aridity it is a very significant fact that Composite dwarf shrubs often become completely dominant as in the transitional areas between grassland and Karroo in South Africa. Many annual and succulent Composites are interspersed, and these and other types of extreme xerophytes

belonging to the family become increasingly characteristic of semi-desert and desert regions. Herbaceous Composites are abundant all over the temperate regions. Annual forms are common as weeds in cultivated land and waste places as well as in desert regions. The annual type of Composite may be looked upon, in a general way, as the most highly evolved of all plants.

The geographical distribution of this great family lends the strongest possible support to the view that the moist tropical forest flora is relatively primitive. The Compositae are not represented there except for one or two subordinate forms. On the other hand, they have everywhere taken possession of the types of habitat which may be regarded as relatively modern. It is interesting to note in passing that Small (1920), who has dealt with the inter-relationships of the tribes, and the evolutionary history of the family as a whole in great detail, regards the family as having had a mountain origin. As we have seen, a great many, perhaps the majority of temperate families, have probably originated on the mountain ranges of the world, often apparently in the southern hemisphere, where the mountain ranges, in Africa at least, being of Permian age or older, have a much longer geological history than in any other part of the world. The various mountain ranges, however, which began to be built up at the close of the Cretaceous, are quite old enough to have seen the origin of much of the modern temperate flora, including the Compositae.

MONOCOTYLEDONS (1950 gen., 26,000 sp.)

The general question of the origin of the Monocotyledons and their relationship to the Dicotyledons need not be discussed here at any great length. Many distinguished authorities have preferred to consider that the Monocotyledons and Dicotyledons represent two distinct lines of evolution, e.g. Kny, Drude, Engler, Warming, Coulter and Chamberlain and others. Many other writers are strongly inclined to adopt the view that the Monocotyledons have been derived from the Dicotyledons. Miss Sargent (1902, 1904) has laid stress on the general tendency towards a geophilous habit among the Monocotyledons, and derives them from dicotyledonous ancestors by means of syncotyly, i.e. the fusion of two cotyledons to form one. Union of the cotyledons to a greater or less extent is seen in many of the Ranunculaceae as well as in other dicotyledons (e.g. *Oxalis*, *Podophyllum*, *Rhizophora*, *Polygonum*). Since such cotyledonary fusion among dicotyledons is accompanied in practically all cases

by shortened and thickened hypocotyls, and by the formation of underground storage organs of some kind or other, Miss Sargent has inferred that the general condition of monocotyledony is associated with a geophilous habit and that, therefore, the Monocotyledons, as a group, have evolved through adaptation as geophytes. The Liliaceae, according to this theory, form the central group among the Monocotyledons.

Considered in relation to our own viewpoint it may be pointed out that underground storage, as indeed storage of all kinds, is usually a response to a resting season. Geophytes are not prominent under uniformly moist tropical forest conditions. Even members of typically geophytic families have little underground storage if they belong to forest habitats in the tropics, e.g. *Clivia, Kniphofia,* etc. Geophytes only become abundant and highly differentiated in subtropical areas with a pronounced resting season. At the same time, a certain amount of storage does take place in subordinate forest species among epiphytes, climbers and forest margin herbs. So our general theory does not require us to argue that Miss Sargent's ideas are necessarily incorrect.

Those who prefer an origin for the Monocotyledons by means of "heterocotyly" (i.e. by the ultimate suppression of one of the cotyledons) connect them through the Araceae, with such typically tropical forest margin herbs as the Piperales (*Peperomia*). This view has been adopted by Hill, Lotsy, Henslow and others. For a fuller discussion of the literature of the subject, Bancroft (1914) should be consulted. Henslow (1893, 1911) looked upon the whole of the Monocotyledons as derived from Dicotyledons through "self-adaptation to a moist or aquatic habit." Most authors are inclined to look upon such tree-forms as do occur among the Monocotyledons as derivative, though there are some, e.g. Lindinger (1910), who regard them as primitive. All these general theories do not really carry us very far.

Whether the Monocotyledons were derived from the Dicotyledons or not, it is entirely in accord with our general theory to suppose that the earliest Monocotyledons were either marsh or forest margin types and, as a matter of fact, this is also in agreement with any of the numerous theories that have been put forward regarding their origin. I have suggested elsewhere (Bews, 1925, p. 46) that if we are prepared to assume that the early Monocotyledons were marsh forms, and they behaved like modern plants of the same type, then they would tend to become widely distributed rather quickly. Marsh

plants and aquatics probably throughout their history have remained to some extent independent of climatic differentiation. It is well known that marsh species tend to be widespread through different climatic areas at the present time. It is not surprising, therefore, to find that among typically aquatic or marsh groups such as the Helobieae, distribution does not throw much light on phylogeny or on their general differentiation. Nevertheless, a careful analysis of the distribution and phylogeny of the different orders of the Monocotyledons does tend to show that as among the Dicotyledons, the influence of the biota under moist tropical conditions has resulted in the production of specialised subordinate types of plant form, and likewise the response to drier and colder conditions has in general meant evolutionary advance.

It is interesting also to note that in their primitive marshy habitats their peculiar habit of growth with underground rhizomes and tufted aerial shoots has enabled many of the Monocotyledons to assume complete dominance while in drier situations the great family of the grasses have succeeded in completely conquering and dominating enormous areas of grassland, a type of vegetation different in many essential features from anything that could have preceded it. This has had a profound effect on the evolutionary history, not only of other derivative types of plant form, but also on the animal kingdom. The grasses, directly or indirectly, are the chief food of nearly all the mammals.

In summarising the distribution, phylogeny and ecological differentiation of the orders and families of Monocotyledons, Engler's system of classification is again followed.

PANDANALES. The screw pines or Pandanaceae (3 gen., 240 sp.) are trees and shrubs of the tropical regions of the Old World. They include some root climbers (*Freycinetia*). They are chiefly forest margin or seashore plants. The Typhaceae (*Typha*, 9 sp.) are widely dispersed marsh plants, while the Sparganiaceae (*Sparganium*, 9 sp.) are also water or marsh forms. Both *Typha* and *Sparganium* go back to the Cretaceous. The whole of this primitive order is, therefore, at the present time, confined to primitive types of habitat.

HELOBIEAE. This large order is also generally considered primitive and is largely aquatic with a few marsh forms. Many of the genera are very widely distributed. The Naiadaceae (*Naias*, 30 sp.) have the simplest flowers, but are very likely reduced types. The Alismataceae (12 gen., 75 sp.) are considered by many to be the most primitive since they come nearest, in many respects, to the Ranales.

The Potamogetonaceae (9 gen., 100 sp.) are interesting because 8 out of the 9 genera occupy salt or brackish water. The largest genus, however, *Potamogeton*, with 90 sp. is chiefly a freshwater type. Of the Hydrocharitaceae (15 gen., 65 sp.), 3 genera, *Halophila, Enhalus*, and *Thalassia*, are marine. The Scheuchzeriaceae or Juncaginaceae (5 gen., 15 sp.) include the genus *Lilaea*, which has a grass-like habit, a caryopsis type of fruit, and the root of the embryo lateral, suggesting in some of its features the grasses, though in others it is remote from that group. It is a North and South American mountain marsh type. Other families of the order are the Aponogetonaceae (*Aponogeton*, 20 sp.) and the Butomaceae (4 gen., 7 sp.). All the Helobieae in their general wide dispersal show how marsh and aquatic forms are largely independent of climatic conditions.

TRIURIDALES. This order includes only the Triuridaceae (2 gen., 25 sp.), a family of Saprophytes found in the tropics, representing another example of response to the influence of the biota.

GLUMIFLORAE. Only the more important points regarding this order will be mentioned here since it is proposed to deal in detail with the important question of the origin and development of the grasses and grasslands in a subsequent chapter. It is significant that the relatively primitive Cyperaceae (77 gen., 3000 sp.) are mostly marsh forms, though it does not follow that they gave rise to the other family, the Gramineae. The Cyperaceae include one woody tropical genus *Schoenodendron* which has a perianth of scales. On the whole, the tropical Cyperaceae, of which the large genus *Cyperus* is representative, with many florets in the spikelet, are relatively primitive, but the family shows early response to temperate conditions in forms like *Macrochaetium* and *Tetraria*, which occur on the mountains of temperate South Africa and in Australia. The South African genus *Schoenoxiphium* is looked upon as the ancestral form of the Cariceae, in which the genus *Carex* has spread all over the temperate regions of the world. The temperate Cyperaceae, then, afford still another example of a probable mountain origin for the temperate flora.

The evolutionary history of the Gramineae (400 gen., 4000 sp.) has apparently followed somewhat similar lines. The Bamboos floristically are undoubtedly relatively primitive, and they have a tropical or subtropical distribution, being largely forest margin types and woody. Marsh forms like the Arundineae (*Arundo* and *Phragmites*), which are said to go back to the Cretaceous, may also be reckoned rather primitive. Early response to temperate conditions on mountain ranges is shown by the tribes Aveneae and Festuceae

with many florets in the spikelets. Reduction in the number of florets goes hand in hand with increased adaptation to drier conditions or colder conditions in subtropical regions and in temperate steppe regions or in the moorland types, etc. in the tribes Andropogoneae, Paniceae, Stipeae, Agrosteae, Zoysieae, Sporoboleae, Chlorideae and Hordeae. The relationship of the tribes, and the detailed course of their probable ecological evolution will be discussed more fully later.

The history of the Glumiflorae illustrates our general theory of response to increasing aridity and lower temperatures exceedingly well in all its details.

PRINCIPES. The Palmae (169 gen., 1200 sp.) have a more definite and reliable fossil record than almost any other group of flowering plants, leaves, fruits and well preserved wood, being found as far back as the Cretaceous in north temperate regions, including Great Britain, far beyond their present range. At present the palms are tropical or subtropical. Like the screw pines probably the most primitive were hygrophilous. Many still grow in tropical swamps and rain forest regions or along river-banks (e.g. species of *Nipa, Bactris, Phoenix, Elaeis,* etc.). Others are very distinctly adapted to dry or even semi-desert regions. The Rattans or Cane palms are climbing forms. Some climb by means of prickles, e.g. *Calamus,* a large genus with nearly 300 species. But thorn development is not confined to the climbing forms. It occurs on the stems and leaves and in the case of *Iriartea* even on the roots. While thorn development, almost universally among the Angiosperms, increases with increasing aridity, some of the palms are apparently exceptions to this general rule. Thorns occur in mesophytic or even hygrophilous tropical rain forest types which do not climb, e.g. *Bactris* and *Astrocaryum,* two tropical South American forms. These facts are important in connection with the ecological evolutionary history of plant forms, which will be discussed more fully later. The exact significance of thorn development is a problem which cannot yet be said to have been satisfactorily solved.

SYNANTHAE. Cyclanthaceae (6 gen., 45 sp.). This small order and family are tropical American and derivative, reflecting, like many of the palms, the influence of the biota. They are plants of palm-like habit, shrubs, climbers, rhizomatous herbs or epiphytes.

SPATHIFLORAE. This order, which is also allied to the Palmae, consists of two families, Araceae (115 gen., 1100 sp.) and Lemnaceae (3 gen., 25 sp.). The Araceae are predominantly tropical and sub-

tropical with a few extensions as forest undergrowth or in moist places through the temperate regions. They consist of climbing shrubs or epiphytes, large or small herbs, often with underground rhizomes or tubers. They are another derivative family in response to the tropical biota and show different stages of ecological differentiation. The climbing shrubs are less specialised than the epiphytes and the herbaceous terrestrial forms are, in many respects, the most evolved of all (cf. Bromeliaceae). They are common around the forest margins or in marshy places in the tropics. Colonisation through hygrophilous habitats has extended into the temperate regions. The genus *Arum* has 15 species in the Mediterranean region and central Europe. *Acorus gramineus* occurs in Japan and the sweet-flag (*Acorus calamus*) is widely dispersed through the northern hemisphere. *Calla palustris* is a marsh plant of Europe, Siberia and North America, while the "Arum Lily" (*Zantedeschia aethiopica*) is common all over South Africa. One species, *Pistia stratiotes*, is a widely dispersed aquatic.

The Lemnaceae (*Lemna*, *Spirodela* and *Wolffia*) are the most reduced of all Angiosperms, small, free-floating, thalloid aquatics. *Wolffia* is the smallest Angiosperm, being little more than one millimetre long and having no vascular tissue. The Lemnaceae are found everywhere except in the arctic zone.

LILIIFLORAE. The Juncaceae (8 gen., 280 sp.), a family of marsh plants of wide dispersal are considered by some to show affinities with the Palmae. Many, though they grow in wet places, are xeromorphic. The interesting South African monotype, *Prionium palmita*, is woody (cf. *Schoenodendron* among the Cyperaceae and the Bamboos among the grasses). Certain other small and rather specialised families of the order are tropical and have responded chiefly to the effects of the biota. The Stemonaceae (3 gen., 12 sp.) are herbs, often climbing with flower-parts in fours and a unilocular ovary of two carpels with one anatropous ovule—obviously a highly evolved family. They occur in the East Indies, Australia and America. The Taccaceae (2 gen., 16 sp.) are tropical, mostly Asiatic and American herbs with tubers. The Dioscoreaceae (10 gen., 240 sp.) are climbing shrubs or herbs with underground tubers or rhizomes, mostly tropical but extending into drier and colder regions, e.g. *Testudinaria* in South Africa and *Tamus communis* in Britain.

All the other families of the Liliiflorae might very well be grouped into a single family. They include the Liliaceae (228 gen., 2600 sp.), the Amaryllidaceae (83 gen., 850 sp.) and the Iridaceae (60 gen.,

1100 sp.) together with the Velloziaceae (2 gen., 70 sp.) and the Haemodoraceae (9 gen., 30 sp.). There are a few tree forms (*Dracaena, Yucca*) which are subtropical. The great African genus *Aloe* is adapted to xerophytic conditions. There are several climbers (e.g. *Smilax, Gloriosa,* many species of *Asparagus*). Some are marsh forms (e.g. *Kniphofia*) and there are many forest margin types as well (e.g. *Clivia*). But the vast majority are geophytes adapted to open grassland or drier subtropical conditions and extending all over the temperate regions as well. Many of the genera are large and widespread (e.g. *Scilla*). Among the Iridaceae, it is interesting to note that probably the most primitive tribe, the Aristinae, have their chief centre of distribution in the Cape mountains with two outside genera (*Eleutherine* in South America and *Orthosanthes* in Australia) another indication that the mountain ranges of the world saw the beginnings of the derivative temperate flora.

Farinosae. The Eriocaulaceae (9 gen., 570 sp.) are a relatively primitive family in this order and are restricted, for the most part, to the warmer regions of the world, their chief centre being tropical America. They have a few extensions into temperate regions and show some connections with the Restionaceae. The Restionaceae (23 gen., 250 sp.) are mostly South African and Australian with a few in New Zealand, Chile, and Cochin China, a family again illustrating the earlier beginnings of a southern temperate flora. Many are marsh forms. Other small families, mostly of marsh plants are the Centrolepidaceae (7 gen., 40 sp.) found in Australia, South America, South-East Asia and Polynesia, the Mayacaceae (*Mayaca,* 7 sp.), American, the Xyridaceae (2 gen., 55 sp.) tropical and subtropical, especially mountainous. The Commelinaceae (29 gen., 320 sp.) are mostly forest margin, marsh or ruderal types in tropical and subtropical regions. The Pontederiaceae (6 gen., 20 sp.) are herbaceous water plants while the Cyanastraceae (*Cyanastrum,* 5 sp.) are an allied small group of tropical African herbs. The Philydraceae (3 gen., 4 sp.) are also herbs distributed from Indo-Malaya to Australia. The Bromeliaceae (57 gen., 920 sp.) are the largest family. The majority are tropical epiphytes, but a few occur on rocks, and two small allied families Thurniaceae (*Thurnia,* 2 sp.) and the Rapateaceae (7 gen., 25 sp.) are tropical South American herbs. The question as to whether many forest herbs may not have had an epiphytic ancestry is worth considering. Recently Goebel (1922) has described velamen on the roots of various terrestrial orchids as well as on *Agapanthus umbellatus, Aspidistra elatior, Crinum longifolium, Clivia nobilis,* all

more or less forest margin types. Velamen also occurs on the roots of grassland terrestrial species of *Eulophia* in South Africa. A typically epiphytic family like the Bromeliaceae, may be more primitive than allied terrestrial herbaceous families. Apart from their mealy endosperm, the Bromeliaceae come fairly near to the Juncaceae among the Liliiflorae, and therefore, may be considered floristically to be rather primitive. Ecologically they are specialised, but epiphytism, like the climbing habit, from which it may often have resulted, may very well have appeared very early in the evolutionary history of the Angiosperms in response to the effects of plant competition and the organic environment (biota) generally. It may be remarked in passing that the terrestrial pineapple (*Ananas*) belongs to the tribe Bromelieae, showing advance in having the ovary inferior, while the other tribes of the Bromeliaceae have the ovary more or less superior.

SCITAMINEAE. This order includes four families with zygomorphic or asymmetrical rather highly modified flowers. They show a tendency towards suppression in the androecium. They are mostly tropical and subtropical plants of the forest undergrowth, forest margins, marshy places or occasionally fairly xerophytic situations which, in their floral structure, as well as ecologically, show response to the influence of the biota (including not only the insect world but, in many cases, birds as well). The Musaceae (6 gen., 58 sp.) approach nearest to the ordinary monocotyledonous type of flower. They are mostly perennial herbs, often large (*Musa*, *Strelitzia*) but some are woody (e.g. *Ravenala*, the Traveller's Tree of Madagascar). The Zingiberaceae (41 gen., 900 sp.) or ginger family are perennial herbs with elongated or tuber-like rhizomes and often thickened roots. Schumann, who dealt with them in Engler's *Pflanzenreich* (1904) points out their similarity in many vegetative characters to the Gramineae and Sargent and Arber (1915) also find affinities in the seedling anatomy of gingers and grasses. The Cannaceae include only the genus *Canna* with 40 species in the warmer parts of America. The Marantaceae (27 gen., 290 sp.) have the flowers most modified of all. They belong chiefly to the American tropics.

MICROSPERMAE. This highly specialised order includes the Burmanniaceae (18 gen., 60 sp.) a family of tropical forest herbs, mostly saprophytes or, in a few cases, root parasites and the Orchidaceae (500 gen., 7500 sp.). The Orchidaceae are a large family of subordinate forms, some entirely dependent as epiphytes or saprophytes, the others dependent as associated plants. The orchids, though

numerous in point of species, are never dominant and ecologically cannot be described as a successful family, since they always play a subordinate rôle in vegetation.

The epiphytic forms are highly evolved as epiphytes, though their origin may be more ancient than the terrestrial forms. The latter, as we have seen, in some cases have velamen, which may indicate that they had an epiphytic ancestry. Comparison of flower structure, however, in the terrestrial and epiphytic forms gives no certain indication of what the course of their evolutionary history has been. All the Microspermae show in the highest degree the effects of the biota and their complex evolutionary history is a very difficult one to disentangle.

SUMMARY

1. The Sympetalae are doubtless of polyphyletic origin and certain of their groups may be more ancient than many of the Archichlamydeae, yet, in a general way, the Sympetalae are recognised as highly evolved. It is significant, therefore, that they are, on the whole, adapted to colder and drier conditions, or in the moist tropical regions are mostly subordinate types, showing response to the influence of the organic environment or biota.

2. Several of their important groups (as among the Archichlamydeae) indicate a mountain origin for the temperate flora, e.g. the Ericaceae and other families of the Ericales, temperate members of the Verbenaceae, temperate families of the Rubiales and Campanulatae including the highest family of flowering plants, the Compositae.

3. Whatever the actual origin of the Monocotyledons may have been, all the available evidence points strongly in the direction of the earlier forms having been hygrophilous, forest margin or marsh types. Such types, at the present time, as doubtless in the past, tend to become very widespread and are relatively unaffected by climatic differentiation. On the whole, therefore, their present geographical distribution does not throw quite so much light on the ecological history of the Monocotyledons as is the case with the Dicotyledons. Nevertheless, here also the influence of the biota under moist tropical conditions has led to the production of advanced specialised types and, in general, climatic differentiation has had an effect. The more advanced types are those which have responded to drier conditions on the one hand, and colder conditions on the other.

4. There are certain indications in the families Araceae and Bromeliaceae, that terrestrial forms may have been derived from epiphytic ancestors. The order of evolutionary development in these cases in response to the biota would be climbing forms—epiphytes—terrestrial herbs. The evidence, however, is not sufficient to enable us to argue that many herbs originated in this way.

5. The detailed evidence among the Sympetalae in support of our general theory is best summarised in the form of a table as in chapter II for the Archichlamydeae.

COMPARATIVE TABLE FOR SYMPETALAE

	Systematic position	Relatively primitive, tropical or subtropical, hygrophilous or mesophytic	Relatively advanced, more temperate or more xerophytic
1.	Dicotyledons	Rutales	Ericales
2.	Primulales	Myrsinaceae	Primulaceae
3.	Myrsinaceae	*Embelia*	*Maesa*
4.	Sympetalae	Primulales	Plumbaginaceae
5.	Sapotaceae	Tropical genera	*Mimusops, Sideroxylon*
6.	Ebenaceae	Tropical genera	*Euclea, Royena*
7.	Oleaceae	Subtropical genera	*Fraxinus*
8.	Contortae	Loganiaceae	Gentianaceae
9.	Contortae	Loganiaceae	Asclepiadaceae
10.	Contortae	Apocynaceae	Asclepiadaceae
11.	Loganiaceae	Loganioideae	Buddleioideae
12.	Asclepiadaceae	Periplocoideae	Other tribes
13.	Asclepiadaceae	Other tribes	Stapelieae
14.	Convolvulaceae	Tropical woody genera	Herbaceous genera
15.	Convolvulaceae	Tropical woody genera	*Cuscuta*
16.	Personales	Solanaceae	Scrophulariaceae
17.	Personales	Verbasceae	Scrophulariaceae
18.	Scrophulariaceae	Tropical trees	Herbaceous genera
19.	Bignoniaceae	Tropical trees	*Rhigozum*
20.	Personales	Bignoniaceae	Pedaliaceae, Martyniaceae
21.	Acanthaceae	Nelsonioideae, Mendonsioideae, Thunbergioideae	Acanthoideae
22.	Lamiales	Boraginaceae	Labiatae
23.	Boraginaceae	Cordioideae, Ehretioideae, Heliotropoideae	Borraginoideae
24.	Verbenaceae	Tropical forms	Temperate forms
25.	Lamiales	Verbenaceae	Phrymaceae
26.	Sympetalae	Personales	Plantaginales
27.	Rubiales	Rubiaceae	Other families
28.	Rubiaceae	Cinchonoideae	Coffeoideae
29.	Rubiaceae	Woody genera	Herbaceous genera
30.	Rubiaceae	Other tribes	Galieae
31.	Dicotyledons	Other families	Compositae

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CHAPTER IV

TREES AND SHRUBS

INTRODUCTION

THE CLASSIFICATION OF PLANT FORMS

THOSE who have dealt with the classification of plant forms (growth forms or life-forms) have hitherto paid little attention to their ecological evolution or, in other words, to their arrangement on phylogenetic lines. The systems adopted by the earlier writers, e.g. Humboldt (1806) and Grisebach (1872), were purely physiognomic. Drude (1890, 1913) has laid stress on two principles, viz. the functional rôle played by any species in vegetation, and its life-history under conditions prevailing in its habitat, with particular reference to duration, protection and propagation. Warming's system (1909) follows similar lines, and in addition he laid stress on "Habitat forms" i.e. general reactions to habitat conditions, particularly to the water factor. Clements, in his later work (1920), states that much the most useful and consistent view of life-forms is obtained from a single point of view—that of vegetation and dominance, and he arranges his different classes of "vegetation forms" more or less in the order of the usual plant successions, beginning with annuals and ending with trees. This arrangement, however, as will be shown more fully later, is more or less the reverse of a true phylogenetic arrangement. Species which appear early in the plant successions are usually modern highly developed forms.

Raunkiaer (1910) by laying stress on the importance of the responses to the resting season, formulated a system which comes nearest to being a truly phylogenetic system, though he himself does not regard it from this standpoint. His class of Phanerophytes or woody plants comes first, and he ends with the highly evolved Therophytes or annual plants. But he falls back in part on a habitat classification and his Helophytes (or marsh plants) as well as his Hydrophytes (or aquatic plants) are not placed in their proper position in an evolutionary scheme of classification. A more important defect in his system is that he did not give value to the effects of the biota. Climbing plants, for instance, he includes among Phanerophytes.

From the standpoint of comparative anatomy, the work of Jeffrey (1917), Sinnott and Bailey (1914) and others lends strong support to the view that, among the Angiosperms, woody types are more ancient than herbaceous. Sinnott and Bailey have also considered the evidence from phylogeny and geographical distribution in support of the view that the tropical woody vegetation is, in general, older than the temperate herbaceous.

In my former work dealing with the vegetation and plant forms of South Africa (1925) the evidence from phylogeny and distribution was examined in some detail, and in addition the concept of primitive unchanging types of habitat as contrasted with more derivative non-persistent types was developed. It was considered reasonable to suppose that the moist-tropical vegetation of Africa, which had apparently remained under its present conditions for a vast period of time and showed connections with the tropical flora of America and Asia, was in general older than the specialised and often xerophytic flora of South Africa. Hygrophilous marsh and stream bank types were also considered relatively old, as well as some seashore types. The mountain ranges were indicated as relatively persistent (at least in the African continent) and the mountain African flora was regarded as a relatively ancient temperate type.

With the evidence from palaeobotany, phylogeny and distribution as set forth in condensed form in the previous chapters, it is now possible to apply those ideas to the world's flora as a whole, and attempt an analysis of the general course of ecological differentiation among the flowering plants, and, as a consequence, the phylogenetic classification of the Angiospermous plant forms. The general lines to be followed by this analysis have already been foreshadowed.

Differentiation under moist-tropical conditions

While moist tropical conditions are relatively constant and unchanging, it must not be assumed that they are absolutely so. Even in tropical rain forest there are some brief periods of relatively drier conditions. Throughout the long past history of our present moist-tropical vegetation it is extremely likely that changes in the inorganic environmental factors have played some part in its ecological differentiation. Otherwise the dominant trees would probably be of a more uniform type even than they are.

The most important factor, however, which has led to the present richness of the tropical flora has been simply the great lapse of time,

combined, of course, with the constant effects of plant competition for space and the biota generally.

There may be something in the idea that favourable conditions in themselves, and apart from the time factor, have led to increased differentiation, that it is when the environmental conditions are as near the "optima" as possible that new species arise most easily, owing to that initial impulse to vary, about which we know so little. Such hypotheses, however, are largely speculative, and very hard to prove. The full extent of the ecological differentiation under uniformly favourable, warm, moist conditions has already been outlined. Trees, subordinate shrubs, lianes, epiphytes and herbs, as well as parasites, saprophytes and peculiarly specialised insectivorous plants have all been produced.

Trees and Shrubs and their Ecological Evolution

The responses to drier and colder conditions have been shown to be, in general, more recent. In the arrangement of our subject-matter in this and the succeeding chapters, the modern vegetation types might have been dealt with in turn, e.g. tropical rain-forest, forest and scrub of drier subtropical, and of temperate regions, grassland vegetation, tundra vegetation, desert vegetation, etc. Constant reference will have to be made to the great geographical climatic areas, in any case, as well as to more specialised habitats, and to the types of vegetation which occupy them. But perhaps the best way of approaching the subject of ecological evolution is to make the plant forms themselves and their evolutionary history the main basis for the arrangement of the facts, and the phanerophytes or trees and shrubs will be dealt with in this chapter.

The trees of moist tropical forest, according to all the evidence already put forward, are to be regarded as the most primitive of Angiosperms. It is therefore important to have clear ideas regarding their main characteristics since they supply the starting-point in the evolutionary history of the more modern types of plant form.

The general characters of Trees and Shrubs of the Moist Tropics

1. Owing to the great lapse of time and the effect of internal factors, as well as under the influence of the biota and, to a much less extent, variations in the inorganic environment, differentiation among tropical trees of moist regions has proceeded very far. Floristically this is shown by the long list of families to which they belong.

Only the most important need be mentioned, viz. Moraceae, Ulmaceae, Olacaceae, Anonaceae, Monimiaceae, Myristicaceae, Lauraceae, Leguminosae, Simarubaceae, Celastraceae, Anacardiaceae, Icacinaceae, Sterculiaceae, Tiliaceae, Guttiferae, Flacourtiaceae, Lecythidaceae, Rhizophoraceae, Combretaceae, Myrtaceae, Araliaceae, Myrsinaceae, Sapotaceae, Ebenaceae, Oleaceae, Rubiaceae. Ecologically, their forms also vary to some extent, though on the whole, they are fairly uniform. They differ in height, they differ in the shape and size and texture of their leaves within certain limits, as well as in other form characters.

2. Flowers and reproduction. The general long-continued uniformity of environmental conditions and the absence of any response to a pronounced resting season are to be correlated with the lack of any marked contrast between the vegetative and the reproductive life of the species. Growth goes on uniformly and steadily more or less all the year round, though there are certain irregular growth rhythms that are not well understood, that are not necessarily synchronous for the different species, and have no relationship to seasonal changes. The period of flowering is far more erratic among the trees of moist-tropical forest than elsewhere. Though many, perhaps even the majority, have more or less fixed periods of flowering, the exact time varies greatly among the different species. Many species, on the other hand, flower at any time of the year. The lack of marked contrast between the vegetative and reproductive life of the species extends also to the spatial relationships between the two, though this applies, to some extent, to more derivative types of trees as well. The flowers of tropical trees are produced in any position, even on the older parts. There is, as a rule, little attempt at localisation. Single flowers or small clusters are common. There are few large conspicuous, dense inflorescences. The evolutionary history of the branching of inflorescences should be analysed in greater detail for the Angiosperms as a whole, but it is among herbaceous and other derivative forms that the more highly evolved types occur. The phenomenon of cauliflory in tropical trees will be referred to in connection with the characters of their bark.

As regards the influence of the insect world on the form of their flowers, a very common idea prevails that the tropical tree flora is one with flowers more brightly coloured, more showy and conspicuous and generally better adapted to insect visits than those of temperate regions. This is entirely a mistake. A glance through the list of families given above should be sufficient to convince the botanist

that conspicuous flowers are very rare indeed. Where such do occur in tropical rain-forests, they belong, as a rule to derivative types, lianes, epiphytes and herbs. Even such derivative types are not floristically so conspicuous as many think. Wallace in his *Essays on Tropical Nature* says, "Conspicuous masses of showy flowers are so rare that weeks or months may be passed without observing a single plant worthy of admiration." "My friend, Dr Richard Spruce, assured me that by far the greater part of the plants gathered by him in equatorial America had inconspicuous green or white flowers."

The main characters of the fruits and seeds of moist-tropical trees must be dealt with briefly though the subject is full of interest. If dispersal is by external means then fleshy fruits and animal dispersal are the rule or the fruits or seeds simply drop from the trees, and are not distributed by any external agency. Wind dispersal could not, in any case, prove very effective in dense tropical rain-forest. The resting period of the seeds is apparently usually a short one, though more exact information on this subject is needed. Guppy believes that vivipary is a primitive characteristic and was at one time more or less universal, but the modern mangrove flora hardly supports this view, since in all other respects than their vivipary the mangroves are rather a specialised and derivative group, consisting of 25 species altogether, belonging to a variety of distinct families which, with the exception of one palm, are all rather advanced members of the Archichlamydeae or of the Sympetalae. Neither floristically nor ecologically (except possibly in their vivipary itself) are the mangroves to be considered primitive.

3. The absence of a pronounced resting season is reflected in the characters of the wood. The trees of tropical rain-forest belong mostly to the "hardwood" class. Many of them have very dense hard woods with a specific gravity greater than 1, so that they sink in water. Now this extreme hardness is impossible in woods where more abundant storage elements are required. The woods of the drier subtropical regions with long, dry winters are, as a rule, much softer and lighter, as are also the woods of temperate trees, though the mechanical elements developed in trees growing in more exposed situations may lead to toughness and "strength" or resistance to tensile stresses. Hardness and toughness of course are not necessarily interconnected in woods. If a single character is needed to serve as a basis for subdividing this fairly uniform class of plant forms, relative hardness in the wood is about as convenient and

suitable as any. A considerable amount of information on this subject is already available in the literature dealing with forestry. Increased softness in the wood is correlated with increased storage in response to colder and drier seasons which, as we have seen, has meant, in general, evolutionary advance. Owing to the fact, however, that (mechanical elements are well developed in the species which grow more isolated and more exposed to the force of winds,) the correlation between relative hardness and softness and the absence or presence of storage tissue in the wood is not necessarily a very exact one. Even granting this, one may still at least maintain that the characters of the wood are probably most suitable for the purposes of ecological subdivision of evergreen tropical trees rather than more superficial characters such as those of the leaves or bark or methods of branching, etc.

4. The trunks of tropical rain-forest trees are not usually so stout as those of equal height growing in more open situations. They grow very tall but remain relatively slender and, as a rule, they require additional support near the base. This is secured by means of plank buttresses or stout cylindrical roots, springing from the stem some distance above the base.

5. Branching. The trees of moist-tropical regions are very sparingly branched. Frequently there are only three grades of branching with the leaves aggregated in tufts at the ends of long bare axes. The number of grades of branching hardly ever exceeds five whereas the trees of temperate and drier regions frequently have seven or eight.

6. The bark of tropical rain-forest trees is thin and poorly developed, sometimes almost transparent, so that the chlorophyll of the cortical layers is visible through it. The absence of a thick bark allows the axillary flower buds to remain dormant for several or many years and then develop, producing flowers on the older parts of the twigs or stem, the phenomenon known as "cauliflory.")Wallace explained cauliflory on teleological lines as an adaptation for pollination by shade-loving Lepidoptera, which do not fly above the canopy of the forest, but it is doubtful whether there is any need for such explanations.

7. Thorn development is very rare, but not altogether absent from tropical rain-forest trees. It occurs in species of *Xanthoxylon*, as well as among subordinate forms, such as certain palms. It is a phenomenon which increases to such a marked extent under drier conditions that the fact that it occurs at all under rain-forest conditions is important and requires special emphasis.

8. The buds of moist-tropical forest trees have rarely, if ever, any covering of dry bud scales, but there is a certain amount of protection by means of stipules, leaf sheaths, or outgrowths of the petiole. There is also often excretion of water, mucilage or resin between the bud and its envelope.) Schimper gives further details and refers also to the peculiar phenomenon of flower-buds being immersed in water or containing water in their calyces until shortly before their anthesis. The lack of very much bud protection is generally to be correlated again with the absence of a prolonged resting season. Whether the possession of rather loosely arranged "naked" buds has any effect on the leaf shape is uncertain or doubtful.

9. Leaves. (Large, simple, smooth-margined, leathery leaves are the commonest type. Compound leaves also are found,) but the percentage of compound leaved forms tends to increase markedly in the drier subtropical region. The most important fact is that the leaves are "evergreen," i.e. they last for more than a year, so that the tree, except in rare cases or under exceptional circumstances, is never leafless and the work of assimilation can be carried on without interruption throughout the year.

The prevalent leathery texture and other xerophytic characters of the leaves of moist-tropical trees have already been discussed in the first chapter of this book in connection with the fossil Angiosperm flora, where the same features were common and characteristic. It was shown to be correlated with relative inefficiency in water conduction through the wood. It may be mentioned in passing that this supplies another argument in favour of using the anatomical characters of the wood as the basis for further subdivision of this class of growth forms.

Apart from their xerophytism, the structure of the leaves of rain-forest species must be correlated in general with their evergreen habit and their relative durability. They carry out their functional activities for a much longer period of time than deciduous species. They are built to endure.

Various teleological explanations of the structural features of rain-forest leaves have been put forward by previous writers. Their coriaceous texture has been supposed to have the purpose of preventing mechanical injury from the very heavy rainfall; such devices as a smooth cuticle, drip tips, channelled nerves and velvety leaves with papillae (the latter chiefly among the undergrowth) have been thought to prevent wetting of the surface and the growth of epiphyllous algae, lichens, fungi and liverworts. Hydathodes are sup-

posed to facilitate water excretion, and to prevent injection of the intercellular spaces of the leaves. Such views were put forward by Stahl, Haberlandt, and Schimper and many others have followed them. They illustrate very well the attitude of most botanists during the years which followed the enthusiastic reception of the principle of natural selection.

The explanations are plausible and likely, yet they are pure guesses, and no attempt was made by those who originated them to connect them with the normal basic physiological processes. Shreve (1914) carried out experimental work in different directions in the montane rain-forests of Jamaica and failed to confirm the view of Stahl that dripping tips facilitate the drying of leaf surfaces. Epiphyllae he found abundant on leaves of every type including those with drip tips. Hydathodes and other supposed adaptional features, Shreve also found, failed to perform the functions attributed to them.

Differentiation under drier and colder conditions

The derivative vegetation of drier and colder regions shows a much greater range of diversity than that of moist tropical regions. This briefly may be considered as due to the following reasons:

(*a*) The internal forces, which lead to differentiation independently of the environment, continue to act.

(*b*) There is increased diversity of the inorganic environment, and the plants have reacted thereto.

(*c*) The effects of the organic environment are still seen, but, in so far as plant competition for space is concerned, this is of decreasing importance the more the forces of the physical environment come into play.

(*d*) The derivative flora has not had a single point of origin or even a few, but has been continually added to by the already rather highly differentiated more ancient, moist-tropical flora. It may be recalled that it was chiefly in the narrower circles of affinity that the warm, hygrophilous types were shown to be phylogenetically more primitive than the types adapted to colder and drier conditions. The latter reflect the varying degrees of differentiation previously undergone by their ancestral forms. The whole problem, therefore, is rather complex and there is a real danger of serious error arising when an effort is made to fit the facts into a single cause and effect relationship between climate and vegetation, as has so often been done. Progress is only possible by continued and careful comparisons

of all different types from every different standpoint both physiological and morphological and by paying attention to phylogenetic history as well as to the reactions and ontogeny of the species.

The physiological facts are the most fundamental. Of course changes of form and structure go hand in hand with changes of function, and form and structure are more easily studied, but Osborn (1925) is probably right when he insists that the ancient dictum of Aristotle holds good, that "Change of function precedes change of form." Function is a more labile thing than form. It is always difficult to separate the two and the study of so-called pure physiology may lead to the adoption of as narrow views as the study of morphology by itself; but teleological reasoning is now generally condemned even though it is difficult to avoid it altogether. It should be supported by experimental work wherever possible.

It is well known that species vary, that the individuals belonging to a species are not all alike. The species of the systematist, moreover, is often found to be made up of smaller units (microspecies, varieties or races). In this connection during recent years a good deal of comparative physiological field work has been carried out in Natal (Bews and Aitken, 1923, 1925). Comparative measurements have been made of the aëration systems of different species, of their transpiration rates, of their water requirements and water deficits at different seasons and under varying conditions, of their rates of water-conduction, etc., combined with examinations of their structural modifications. The result of it all has been to indicate that very likely physiological races may be recognised, which do not differ in, at least, any very obvious or easily recognisable structural features. Species (e.g. *Ptaeroxylon utile*) may grow in mesophytic or even hygrophilous forest or may be found outside the forest in extremely xerophytic situations. A long series of experiments, carried out by Aitken, showed that this species, as represented in the drier parts, possessed a remarkable power of lowering the water content of its leaves (i.e. of tolerating a high water deficit) without injury. It is very difficult to be sure that structural modifications are not involved but it can at least be said that physiological processes apparently change without any obvious changes of structure.

Our experiments showed further that, while the species which appear relatively late in the plant succession are usually very rigid in their requirements and show a small range of variation in their physiological processes, the species which act as pioneers or appear early in the plant succession are much more plastic physiologically.

But the climax species belong to more primitive types of plant form than the pioneer species. An increase of physiological plasticity, therefore, has been one of the trends of evolutionary development.

The first evolutionary change shown by primitive tropical species was probably the initiation of the process of acquiring this greater degree of plasticity in their physiological behaviour. Structural changes followed. A long time probably elapsed before the various efficient modern types of plant form were produced. Important alterations took place in their anatomy, in the characters and arrangement of the conducting elements, in their storage tissues, etc. as has fully been recognised by Jeffrey and others, whether they are right or not in the details of their analyses of the order of the changes.

The main contribution which can be made to this subject by our present studies in ecological evolution consists of a comparison of the moist tropical types already described with the types adapted to drier conditions on the one hand and to colder conditions on the other. Since the latter are both relatively modern forms the differences illustrate various evolutionary trends. Reactions to drier conditions and to colder conditions have much in common. In both cases it is the necessity of providing for a resting season that has led to the most fundamental changes. But there are also differences between the reactions to the different main types of climate. As a matter of fact, the subdivision of the derivative types can be carried rather far, but our space is limited and only three main evolutionary trends will be dealt with here, as follows:

(1) The responses seen in the trees and shrubs of tropical and subtropical regions with dry seasons, culminating in the extreme types of woody xerophytes found in desert regions.

(2) The differentiation of warm temperate sclerophyllous vegetation occurring in regions of wet winters and dry summers.

(3) The differentiation of other temperate woody vegetation.

EVOLUTIONARY TENDENCIES IN THE TREES AND SHRUBS OF DRIER TROPICAL AND SUBTROPICAL REGIONS (REGIONS WITH DRY WINTER SEASONS, SEMI-DESERTS AND DESERTS)

1. Floristically the families represented are more advanced. This has already been sufficiently emphasised in the preceding chapters.

2. Flowers and reproduction. The well-marked seasonal growth rhythm is reflected in the increased localisation in time and, to some

extent, in space, of the reproductive processes. The majority of the species flower in spring at the beginning of their new period of growth. Conspicuous flowers are more common, especially among shrubby forms. Wind dispersal of fruits and seeds becomes fairly common. The seeds are more viable.

3. The woods of the trees and shrubs in regions where there is a pronounced dry resting season show a much greater range as regards hardness. A few are fairly hard, but the majority are much softer than the woods of moist-tropical forest trees. The increased softness is chiefly to be correlated with the development of parenchymatous storage tissue in the wood.

4. There is a general reduction in height among derivative forms which reflects fairly accurately and proportionately the increasing aridity, though, in the previous history of the various species, the action of the biota may have been partly responsible for bringing it about. There is not, however, a proportionate decrease in the diameter of the stems with decrease in height. On the contrary, trees growing in more open situations usually have widespreading branches and foliage and much stouter trunks than those of tropical forest. This is usually explained as a response to the light factor (which is, of course, important). But it is explained more comprehensively by reference to the effects of the biota generally. Tropical species grow tall and slender because success in plant competition depends more than anything else on ability to grow tall. With decreasing effects of the biota trees grow as large as possible but not necessarily as tall as possible. Of course there is a limit to the size they can reach even under favourable conditions and in the absence of competition, depending largely on the mechanical difficulties of their organisation, but this limit, in the case of many spreading giants of subtropical regions, is a rather high one.

Since the stems of trees in more open situations are stouter, there is not the same need for extra support and buttresses, supporting roots, etc. are not as a rule developed.

5. Decrease in height is usually associated with increase in branching. In many forms the branching takes place a few feet above ground, giving a short trunk and a very spreading, umbrella-like canopy—the "flat-crowned" type characteristic of open savannah forest in subtropical regions. It is a form well suited to withstanding winds but very badly adapted to withstanding the weight of snow. Snowstorms occasionally occur in Natal and I have somewhat vivid recollections of the absolute devastation caused by a not very heavy

fall of snow among the flat-topped trees of the Thorn Veld (*Acacia* spp. dominant).

6. With further decrease in height combined with increase in branching the tree form passes into the shrub form. A continuation of the process produces dwarf-shrubs, suffrutices, under-shrubs and finally herbs. Even within the limits of a single genus (e.g. *Euphorbia, Hibiscus, Solanum,* etc.) the whole range of forms may be found. The lower-growing shrubby and herbaceous derivative types will be dealt with in greater detail later.

7. There is a general decrease in size of the leaves with increasing aridity which, on the average, is very well marked but is not quite universal. Hereditary influences play a part and a few trees of open forest have large leaves. (See statistical comparisons given in the first chapter.)

8. The percentage of species with compound leaves tends to show decided increase, with increasing aridity. Since the separate leaflets are the assimilating units, leaf division has more or less the same effect as reduction in the size of the leaves.

There have, however, been many teleological guesses at the significance of compound leaves. Schimper refers to their mobility and Cowles (in vol. II of the Chicago Textbook, p. 551) supposes that divided leaves are peculiarly favourable for the sifting of sunlight and for increasing the aggregate surface illuminated. Apart from the fact that no proof is offered for such hypotheses, the evidence already mentioned that leaf division tends to increase among types occupying open sunny situations would tell against the suggestion put forward by Cowles. It is the trees of dense tropical forest that require to increase as much as possible the aggregate amount of illumination, not the trees which grow in the open, fully exposed to full tropical sunlight.

9. Leaf-fall. This is one of the most obvious of the external signs of a seasonal periodicity. In the regions of dry winters the deciduous tendency varies among different species and among individuals of the same species. Though it involves structural changes, leaf-fall is quite comparable with the physiological processes already discussed, which vary without any very apparent corresponding morphological changes, and it is interesting to find that here also some species or races are far more plastic than others. The primitive moist-tropical forms, as we have seen, sometimes show irregular deciduous tendencies.

10. Where the deciduous habit has become fixed, it is correlated with changes in the architecture of the leaf. Deciduous leaves are

not built to endure. They are thinner and flimsier and usually have straighter main veins than evergreen leaves. The changes undergone in preparation for the actual process of leaf-fall itself are well known and need not be described in detail. But a very useful piece of work would be a more detailed comparison, both physiological and morphological, than has so far been undertaken, of the deciduous and evergreen types of leaves.

11. Bud-protection especially in the case of foliage buds is more pronounced in the drier regions than in the moist tropics. Bud scales are often present and are sometimes very thick and well developed.

12. A thick bark is a common feature of the relatively more xerophytic tropical and subtropical trees, forming a marked contrast with the thin smooth bark of moist-tropical forest trees. Priestley and Woffenden (1922) quote Douliot as calling attention to the marked effect of light on the formation of periderm in the stem. Priestley (1921) also refers to work carried out in his laboratory on the rôle played by sunlight in causing the rapid condensation of phellonic acid, one of the suberogenic acids concerned in cork formation, but he is inclined to attribute increased cork formation under increased insolation to the more rapid evaporation from the stomata and the consequent early blocking of the sub-stomatal apertures. The blocking is followed by accumulation of sap which is followed again by the appearance of a meristematic phellogen.

Whatever the underlying causes, there is no doubt that extensive cork formation is favoured by the open sunny situations which are occupied by the derivative subtropical trees. Constantly recurring grass fires, which, without doubt, are often caused by natural agencies, and have, therefore, been a factor of some importance ever since the establishment of extensive areas of grassland, are also said to cause increased cork formation in woody species occupying grassland habitats. Whether this direct effect of fire has in course of time become hereditarily fixed is, of course, much more difficult to prove and would, by most botanists, be considered unlikely.

13. Lignification from the physiological standpoint is still a very obscure process. The importance of lignified tissues in giving strength and rigidity is sufficiently obvious and is dealt with very fully in such works as that of Haberlandt. More attention might with advantage be directed to the phylogenetic aspects of physiological anatomy, but we can hardly enter into a discussion of the subject here. According to Jeffrey's ideas lignified tissues in the stem (the tracheids) have, in the course of time, been transformed into storage paren-

chyma. Increased storage is, of course, one of the most important results of a dry resting season and, as we have seen, often leads to the production of a softer type of wood.

On the other hand, there is an increase of lignification in the leaves of many evergreen xerophytic forms. It has been suggested by Guttenberg (1907) that increased lignification in leaves plays an important part in preventing deformations of the cells and softer tissues. It also prevents fatal injury when the water deficit is increased. Experiments carried out in Natal (Bews and Aitken, 1923) have shown that there is a rough agreement between increased lignification in leaves and a slower rate of drying out, though the agreement is not altogether a close one and doubtless other forces are at work as well. Increased lignification, as a rule, goes hand in hand with decrease in size of the leaves culminating in the ericoid form which, though it occurs in drier subtropical regions, is more characteristic of mountainous and temperate vegetation. Increased lignification among xerophytic tropical or subtropical types often results in a complete transformation of the organ concerned, and a loss of the original function in the production of thorns.

14. Spinosity. Thorn development, as already mentioned, increases more or less in direct proportion to increased aridity. In many desert regions practically all the woody species are thorny. But species are usually very plastic in this respect, as plastic as they happen to be in their water requirements. A few species may even be entirely thornless or very thorny according to the situation in which they grow. Lothelier's experiments (1890–3) have shown that in moist air or in feeble light normally thorny species like *Ulex* can become leafy and thornless.

When there is increased vigour of growth as on coppice shoots or when thorny species are kept cut back and there is, in consequence, an increased water supply to the shoot system from the relatively large root system, then the thorns are often much larger and more prominent than usual. While thorn development may be regarded as the final visible result of the increased lignification which appears to result from increased aridity, a full understanding of the cause of their formation will probably have to await a better knowledge of the process of lignification itself. But from the natural selection standpoint there is no doubt that the presence of thorns serves to protect plants against grazing herbivores. Botanists, however, as already pointed out, are no longer completely satisfied by such teleological explanations.

15. Succulence. From the physiological standpoint more attention perhaps has been paid to succulence than to any of the other evolutionary trends among Angiosperms, especially by Dr Macdougall and his associates, e.g. H. A. Spoehr in his elaborate researches on the carbohydrate economy of the Cacti. The pentose series of sugars, though present in varying amounts in all plants, constitute, at times, more than half the total sugars of the Cacti. While the simpler sugars decrease with drying, the pentosans increase decidedly. Researches of this kind are, of course, of fundamental importance. Moreover Macdougall's dendrograph records show that daily variations in the size of the stems of succulents are approximately the reverse of those occurring in woody trees and most herbaceous plants. Swelling begins in succulents in mid-forenoon while the stomata are closing and continues until nearly midnight, when the stomata open. After midnight contraction sets in and continues until forenoon. Ecologically succulents are characterised chiefly by their large water balance on which they draw during dry periods. There are, however, few tree succulents; the Cacti in America and the genus *Euphorbia* in Africa are the best known examples. The vast majority of succulents are more or less herbaceous. All succulents are highly evolved not only ecologically but also floristically.

16. Increased osmotic pressure in the cell-sap is an important feature of plants of drier regions and especially of desert plants as has been shown by the work of Fitting (1911), of Iljin, Nazarova and Ostrovskaya (1916), and of Harris and various co-workers in America (1916, 1917). The last mentioned have published numerous important papers on this subject.

17. Minor xerophytic features among this derivative class of plant forms need not be dealt with in detail, e.g. protection to the stomata, coverings of leaf-surfaces, etc. Most of them have been explained on teleological lines, but there is room for much further experimental work, which might throw light on their relationship to the basic physiological process and on their origin and evolutionary history in each case.

Sclerophyllous Vegetation

The type of vegetation termed "sclerophyllous" by Schimper is found in the Mediterranean region, in California, in the south-west of South Africa, in the south-west and south of Australia and in Chile. In general it is a type adapted to wet winters and dry summers, but both in America and in Africa it tends to spread along the moun-

tain ranges into regions of wet summers. It differs chiefly from the vegetation of regions with dry winters or very cold winters in being evergreen. Though derivative, it is in many respects an older type than that of dry winter regions. It is separated from the moist-tropical by a wider gap. It contains many floristic elements that do not connect very closely with tropical types, e.g. Proteaceae, Ericaceae, etc., though in other cases its tropical origin and derivative character is clearer, e.g. in the Compositae, Leguminosae (Papilionatae), Rosaceae, Geraniaceae, etc. Trees are rare, but those that do occur have closer tropical affinities than the typical Macchia shrubs, e.g. *Olea, Laurus, Ocotea, Olinia, Gymnosporia,* etc. Its general floristic composition and connections with the primitive allied tropical types have been mentioned in the survey of the families given in the previous chapters. There are many indications that it represents the earlier responses to temperate conditions, and began on the mountain ranges of the world probably as early as Cretaceous times.

The climate of the regions with sclerophyllous vegetation possesses the following features. The winters are mild; frosts, if they occur, are not severe and only at higher altitudes does snow fall. The rain falls mostly in winter, but the rains though heavy are not of long duration. There are plenty of intervals of bright sunshine and growth can continue throughout the winter. The summers are much drier, but growth does not cease in the dry season, since there is still a supply of water in the soil, even though the water table does gradually become lowered. The most important feature of the climate, then, is the absence of a really pronounced resting season in spite of the increase of general xerophytic conditions. The textbooks in dealing with this type tend to lay too much emphasis on the summer drought which Warming describes as hostile to vegetation. It certainly leads to an increase in xerophytism, but it is the absence of a complete resting season that explains the retention of the evergreen habit. In the colder temperate regions evergreen shrubs, e.g. the heathers, are also distributed over regions of relatively mild wet winters.

Evolutionary tendencies among Sclerophyllous Types

1. A deep and extensive root-system in proportion to the size of the plants is more or less a universal characteristic. This is to be correlated with the gradual lowering of the water table as summer advances.

2. There is a marked reduction in size of the species. Trees are rare and tall trees do not occur. Yet, though much reduced in size,

the majority of the species remain woody even among typically herbaceous families like the Compositae. The dominant shrubs of Macchia reach a height of about twenty feet. Lower-growing heather-like forms appear in the earlier stages of the plant succession.

3. The decreased size is again associated with increased branching. Often the branching is of a dense rigid type.

4. The wood of the species tends to be rather hard and tough.

5. The leaves are sometimes flat and leathery, but in the majority are very much reduced in size and are often of the ericoid type. Heath-like forms belong to a number of widely separated families, e.g. Rosaceae, Leguminosae, Grubbiaceae, Santalaceae, Penaeaceae, Euphorbiaceae, Polygalaceae, Rutaceae, Empetraceae, Bruniaceae, Thymelaeaceae, Verbenaceae, Labiatae, Compositae, Epacridaceae, Ericaceae and others.

The marked reduction in size of the leaves is to be correlated probably chiefly with the retention of their evergreen habit. The species have to withstand long periods of adverse conditions due to dryness or low temperatures. Attention has been directed to the ericoid forms chiefly as represented in the cold temperate regions by such types as *Calluna*. The ericoid type is much more richly represented on the mountains and warm temperate regions of Africa where much older phylogenetic forms occur. The Ericads of north temperate regions are a few outlying derivative forms. Physiological explanations should pay more attention to the previous phylogenetic history of plant forms. Yet Schimper's idea of the "physiological drought" supposed to exist under peaty conditions is supported by many. Clements has shown that the peaty soils of moorlands are deficient in aëration, and are thus unsuitable for the development of normal root systems, a factor no doubt of importance as far as plants like *Calluna* are concerned, but it does not apply to the hundreds of ericoid forms at the Cape which have very deep roots. Priestley (1924) finds that moorland peaty plants form usually large quantities of fats in their roots and from such fatty substances abnormally thick cuticles are formed in the shoots and leaves as well as abnormally early secondary endodermis, cork, etc. He thinks that the early formation of a thick cuticle, etc. may profoundly modify the forms of leaves, and the structure of the shoot generally. All this may be true, but the great majority of ericoid forms do not occur on peat. F. C. Gates (1914) laid emphasis on the necessity for keeping the transpiration within the limits of absorption during winter as the factor explaining xerophily in ericoid forms. Water loss in winter

is low, but in evergreen forms it continues to take place even when the water is frozen round the stem and roots. Work of this kind is very useful as showing how ericoid forms have been able to take possession of the habitats they occupy in north-temperate regions, but it does not, of course, explain how the form has been produced. Nor are any attempted correlations between peaty or moorland conditions and the ericoid habit ever likely to explain things fully, since the ericoid form is almost certainly far more ancient than northern peat moors. The whole problem could best be studied at the Cape, where such a multitude of ericads are found belonging to very diverse circles of affinity. It would be very interesting to know how many of the ericoid forms in the separate families mentioned above show the same type of metabolism leading to an accumulation of fats as described by Professor Priestley.

6. Compound leaves are rare among sclerophyllous types in contrast to the drier subtropical vegetation.

7. Lignification. As the name "sclerophyllous" implies, lignification in the leaves is greatly increased. The significance of this has already been discussed. It is much more common in this class of forms than among the drier subtropical types.

8. The bark of sclerophyllous trees and shrubs is well developed.

9. Bud protection by means of bud scales is not prominent; in fact bud scales are rare. This, as in their evergreen habit, is a feature in which sclerophyllous forms come nearer to the primitive evergreen tropical species.

10. Spinosity is also rare, though the margins or apices of the leaves are often prickly.

11. The osmotic pressures of the cell-sap are high.

12. Succulence is very rare.

13. Ethereal oils are a feature of quite a large number of sclerophyllous forms, especially the Rutaceae and the Labiatae. Dixon's experiments have shown that ethereal oils tend to retard water loss.

14. Minor xerophytic features are common. Thick cuticles are more or less universal, hairy or woolly coverings to the leaves are very common, as are sunk stomata, etc. The leaves are often placed so as not to expose their broadest surfaces to the sun. Many of the leaves are bluish in colour. Schimper, who is followed by Warming, states that the intercellular space systems of the leaves are poorly developed, but our experiments on Natal species by injection methods have shown that mere examination of sections is not to be trusted in arriving at conclusions on this subject.

TEMPERATE WOODY TYPES

The characters of the temperate vegetation are influenced chiefly by the low winter temperatures which lead to a resting period similar to that of the drier subtropical regions. If the winters are dry as well as cold, the winter rest is emphasised, and in the great open Steppe regions woody plants are very rare or absent, the vegetation consisting of grasses and associated herbaceous forms. A winter covering of snow serves as a protection to plants, and the vegetation of regions with winter precipitation does not show such extreme response to the resting season. Evergreen shrubs are able to survive. If the winters are relatively mild and wet without much snowfall, evergreen shrubs may be dominant as in the case of heathers in moorland regions.

In the temperate regions of eastern Asia and Japan, where the record has not been interfered with by the Great Ice period, as has happened so comparatively recently in Europe, the transitions from tropical to temperate are gradual, and in North America where the land connections with the tropics are more open the same statement, to a less extent, applies. The temperate deciduous trees connect with the drier subtropical types rather than with the sclerophyllous types. The reactions to low temperatures are very similar to the reactions to dry winters. The seasonal growth rhythms, however, are more pronounced in temperate trees than in the subtropical. The deciduous habit, in consequence, has become more definitely fixed. The reserve substances often undergo changes during the resting season. As winter approaches, the abundant starch is converted into fats or sugars. Starch is reformed in spring prior to being redissolved and used in the formation of new growth. The growth rate of temperate trees is increased in summer by the longer daylight, a fact which tends to emphasise still more the seasonal contrast.

EVOLUTIONARY TENDENCIES AMONG TEMPERATE TREES AND SHRUBS

1. The temperate trees and shrubs are very few in number as compared with tropical and subtropical. The temperate woody genera are much smaller than those of tropical and subtropical regions (e.g. *Eugenia, Eucalyptus*) or even warm temperate sclerophyllous genera (e.g. *Erica* and *Rhododendron*). Their small numbers and the few species in the genera may be correlated with their relatively short evolutionary history. Such fossil representatives of the same

genera as do go rather far back were nearer to the warm temperate and evergreen than the cold temperate and deciduous.

2. Like the subtropical forms they show reduction in height and have stout trunks with increased branching. Their woods are softer than the tropical, though they are usually strong and tough with the mechanical elements well developed. They are harder than many of the derivative subtropical forms. The resistance to winds is more important in the temperate regions.

3. Their leaves are more distinctly modified in response to the fixed deciduous habit. They are thinner, more translucent, more membranous, with usually straighter veins. Preparation for leaf-fall by means of an absciss layer takes place at a relatively early stage in their life. They are built to be used for a short time and then discarded. Their autumn colourings provide a scene never to be observed in the tropics. A very high percentage of them have toothed margins as compared with the trees of tropical forests. They are somewhat smaller in size than the average of tropical forms but marked reduction in size is not a feature of deciduous leaves.

4. Unlike the warm temperate evergreen species and many of the tropical and subtropical, increased lignification is not a feature of the leaves of temperate trees. This is to be correlated again with their fixed deciduous habit.

5. Compound leaves are commoner than among the purely tropical or evergreen warm temperate, but not so common as among the drier subtropical types.

6. Bud protection by means of bud scales is very pronounced.

7. The bark of temperate trees is fairly well developed.

8. Spinosity is rare in contrast with the drier subtropical trees and shrubs.

9. Succulence is not a feature of temperate woody types.

10. Evergreen trees are rare in cold temperate regions and such as do occur are confined to the more favourable situations. Evergreen shrubs are common in the regions of relatively mild wet winters. All this class of cold temperate evergreens are here regarded as derivative from the warm temperate woody vegetation whereas the deciduous cold temperate trees are considered to be more nearly allied to the subtropical forms of dry winter regions.

In conclusion, however, it may be repeated that while it has been found convenient to separate the responses to dry subtropical conditions, to warm temperate conditions with wet winters and dry summers, and to cold temperate conditions, these responses have

much in common and are not fundamentally different from one another. They all depend on various slow changes in the basic physiological processes followed by structural changes which have taken place in the course of the evolutionary history of the Angiospermous tree form. Climatic differentiation has led to a certain amount of sorting out of the increasingly diversified forms, but the beginnings of most of the changes can be seen under the relatively constant and very ancient moist-tropical conditions.

SUMMARY

1. In this chapter an attempt is made to trace some of the main ecological evolutionary tendencies among Angiospermous trees and shrubs. The moist-tropical tree type is the most primitive, but during the long period of relatively uniform favourable conditions under the influence chiefly of the biota but, to a much less extent, also, doubtless, through minor changes in the inorganic environment, a considerable amount of differentiation has taken place, as is shown by the list of families to which such forms belong. The contrast between vegetative life and reproductive is not well-marked; their flowers are usually inconspicuous and are produced irregularly at varying seasons of the year; capsular fruits and wind dispersal of seeds are very rare; their seeds are probably not usually very viable. Their woods are generally hard with little storage parenchyma; their trunks are tall and slender, usually supported at the base by buttresses of one kind or another; they are not much branched. Their bark is very thin; thorn development is very rare; their buds are of the "naked" type. Their leaves are usually large, simple, smooth-margined, somewhat leathery and evergreen.

2. Under drier and colder conditions the effects of the inorganic environment become more marked while the biota has less influence. Emphasis is laid on the fact that physiological changes probably preceded structural changes.

3. Derivative types of trees and shrubs all tend to show to a greater or less extent such features as the following (*a*) a greater localisation of the reproductive processes both in time and space, (*b*) the production of softer types of wood, (*c*) a general reduction in height though not necessarily in the diameters of their stems, (*d*) an increase of branching, (*e*) a decrease in size of their leaves, (*f*) increased bud protection, (*g*) thicker bark, (*i*) an increase of minor xerophytic features.

4. Other responses, however, differ according to the nature of

the climatic changes. In subtropical regions with dry seasons, with increasing aridity the deciduous habit is adopted or, if the leaves remain evergreen, they are much reduced in size. Lignification in the assimilating organs is often increased. Under semi-desert or desert conditions thorn development is abundant. There is a marked increase in the number of compound-leaved forms. Succulence is a feature of many forms. Increased osmotic pressure in the cell sap is common.

5. In regions with wet winters but dry summers the species remain evergreen but reduction in size goes further. Trees are rare and sclerophyllous shrubs are dominant. They have very deep root systems. Their leaves are much reduced in size and, in a great many widely separated circles of affinity, ericoid forms have been produced. Lignification in the assimilating organs is still more pronounced, but features such as spinosity and succulence are rare. A large number produce ethereal oils and minor xerophytic features are common.

6. Cold temperate trees and shrubs are mostly deciduous and connect with the drier subtropical; a few (mostly shrubs) are evergreen and connect with the sclerophyllous vegetation of regions of dry summers.

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CHAPTER V

DERIVATIVE TYPES PRODUCED UNDER MOIST FAVOURABLE CONDITIONS

It has already been pointed out that Raunkiaer's system of classifying the life-forms of plants does not lay sufficient stress on the influence of the biota. It has also been shown that, under moist warm conditions, this has been of paramount importance in bringing about differentiation among the most primitive type of Angiosperm. The trees themselves show its effects. They are not all of equal importance from the standpoint of dominance. In moist tropical forest they tend to form several canopies, and those of the lower canopies are, to some extent, dependent on those of the upper canopy. It is unfortunate that we know so little regarding the development of, or plant succession in, tropical rain-forest. The absence of anything approaching pure dominance of single species is, of course, well known, but the exact successional relationships of the extraordinarily mixed assemblage of trees has never been analysed, or at least not in sufficient detail to be of much assistance from our present standpoint.

In dealing with the more distinctly modified types of plant form, however, our task is simpler, and the more important of these will now be dealt with, in each case somewhat briefly.

Lianes. The term liane, at one time applied only to woody climbers, is now generally used for the whole group of climbing plants. H. Schenck is quoted by Schimper as giving an estimate, which probably errs in being too low, that over 90 per cent. of all lianes are tropical. Woody lianes are very rare outside the tropics, the extra-tropical climbers being mostly herbaceous or thin-stemmed derivative types. From the physiological standpoint, lianes differ markedly from the trees over which they climb, in their semi-dependent mode of life. The correlations between this and their morphological modifications are fairly obvious. The internal structure of their relatively thin stems provides for as efficient conduction as possible, combined with strength. Their undulating method of growth, together with such special modifications as hooks, spines, prickles and tendrils of various kinds, prevent their slipping downwards.

Their relationships to the light factor are most important. Often their juvenile stages of growth differ markedly, particularly in their leaf-forms, from the adult stages of their development after they have overtopped the trees and reached full sunlight.

Their study is full of ecological interest from many different standpoints. Their effects on the forest, as a whole, are most marked. They tend to stifle all other forest plants by their abundance and rank growth and shading effects. Since they do not require to use the material they form to build up stout stems, as a support for their foliage, they possess an enormous advantage from the standpoint of economy of effort. In themselves they represent one of the most interesting directions in which evolutionary differentiation has progressed. But, further, they react on the other types, and particularly on the trees over which they grow. They weaken the trees and, assisted by fungal or other parasites, hasten their death. With the death and collapse of the trees open gaps are formed and a renewed struggle for the space left vacant is initiated among the seedlings of the various species present. Thus the process of differentiation in the forest vegetation as a whole is accelerated. The process illustrates very well the "action, reaction and interaction"—to use Osborn's phraseology—of the various evolutionary forces and it demonstrates particularly the outstanding importance of the organic environment under conditions where the inorganic factors are relatively uniform and favourable.

Lianes belong to a large number of diverse families, including the Moraceae (*Ficus*), Aristolochiaceae, Piperaceae (*Piper*), Menispermaceae, Magnoliaceae, Anonaceae, Pittosporaceae, Cunoniaceae, Connaraceae, Leguminosae, Malpighiaceae, Trigoniaceae, Polygalaceae (*Securidaca*), Dichapetalaceae, Euphorbiaceae, Sapindaceae, Hippocrateaceae, Icacinaceae, Sabiaceae, Rhamnaceae, Vitaceae, Dilleniaceae, Marcgraviaceae, Passifloraceae, Ancistrocladaceae, Combretaceae, Araliaceae, Apocynaceae, Asclepiadaceae, Convolvulaceae, Bignoniaceae, Acanthaceae, Cucurbitaceae, Compositae, Palmae (*Bambuseae*), Gramineae, Cyclanthaceae, Pandanaceae, Araceae, Liliaceae, Dioscoreaceae, Orchidaceae (*Vanilla*).

This long list shows clearly that lianes have been produced all through the long history of Angiosperm differentiation. The climbing habit in itself, of course, is much older than the Angiosperms, and there is no reason why many lianes should not have appeared very early among the flowering plants.

THE ECOLOGICAL EVOLUTION OF CLIMBING PLANTS

The classification of climbing plants, usually adopted in the text-books, is made to depend too much on the modification of various organs which assist in climbing. It is doubtful whether this has more than a very general significance. Among lianes, as among other plant forms, the evolutionary trend has been from the woody to the herbaceous and from the hygrophilous or mesophytic towards the xerophytic. The following classes are arranged in a rough evolutionary sequence.

1. Woody scramblers. This large class of tropical lianes are particularly interesting because so many of them are sufficiently plastic to show very well the origination of the climbing habit. One of the best examples is the South African species *Scutia commersoni* (*S. indica*). In the absence of support it grows often as a rather stout-stemmed tree, sometimes it is a much branched erect shrub, but usually, when it gets an opportunity, it becomes one of the loftiest lianes or "monkey ropes" of the forest. Species of *Dalbergia* and many others behave more or less in the same way. Examples may be found of individuals which begin life, and continue for many years growing erect, and self-supporting, and afterwards produce climbing branches which overtop the neighbouring trees.

2. Woody lianes, in which the climbing habit has become fixed, show more definite modifications. Their stems are thin and often wavy and organs are frequently modified to assist in climbing. "Watchspring" tendrils are common.

3. Mesophytic half-woody or perennial herbaceous lianes. This class is of a distinctly more advanced type and is also more heterogeneous. It may be subdivided according to the methods of climbing that have been adopted, though it is difficult to decide which of those are to be reckoned relatively primitive. Probably they represent diverging lines of ecological differentiation. (*a*) Root climbers have horizontal anchoring roots often very tough and fibrous, as well as positively geotropic absorbing roots with well-developed conducting elements. (*b*) Twiners are on the whole more characteristic of open situations or of temperate regions and probably represent a fairly advanced type. (*c*) Tendril climbers have various organs modified. The degree of modification, of course, gives some indication among allied species as to relative advance but not much stress is here laid on such somewhat superficial phenomena. Even many of the woody lianes have their branches or other organs modified to assist in climbing.

4. Herbaceous geophytic lianes. This class combines underground storage with the climbing habit. The aerial climbing stems are often annual. The Dioscoreaceae are the best examples. They are characteristic of regions where the vegetation shows response to a resting season.

5. Xerophytic lianes. In the drier subtropical regions, where succulent and thorny scrub is the dominant type of vegetation, many xerophytic lianes occur. The family of the Asclepiadaceae contains numerous examples, but others occur in a variety of other families, e.g. Euphorbiaceae, Vitaceae, Cucurbitaceae, Compositae (*Senecio*), Liliaceae (*Asparagus*), etc. Many are succulent, others have reduced leaves, etc.

6. Therophytic (annual) lianes. These are all herbaceous and though some, e.g. among the Cucurbitaceae, reach surprisingly large dimensions yet the majority are small forms. As in the case of all annual herbaceous types they represent a modern development.

7. Transitions to herbaceous non-climbing types. Around the margins of forests, in grassland areas, on sand-dunes, in waste places, cultivated land, etc., there are many prostrate creeping plants which connect fairly clearly with climbing forms. In families like the Cucurbitaceae, Passifloraceae, Convolvulaceae, where the vast majority of the species are climbers, the origin of the few straggling creeping types is fairly obvious. It can be studied also in certain large genera, such as *Thunbergia* (Acanthaceae), *Cissus* (Vitaceae), *Ipomaea* (Convolvulaceae), etc. While the evidence is entirely insufficient to allow us to argue that all creeping forms originated in this way, there is little doubt that the climbing form, in many cases, represents an intermediate stage in the evolution of the terrestrial herb from woody ancestral forms. It may here be remarked that, from their studies of comparative anatomy, Jeffrey and his pupils, e.g. Eames (1911), as well as Sinnott and Bailey (1914), are apparently of the same opinion, though the latter authors differ from Jeffrey in the details of their interpretation.

Epiphytes. The extraordinary abundance of epiphytes in tropical rain-forest is noted by all explorers of such regions, but they hardly occur outside the tropics, and moist subtropics. They represent a specialised class of derivative forms which have responded to the effects of the organic environment. Schimper (1903) has classified them into (*a*) Proto-epiphytes, (*b*) Hemi-epiphytes, (*c*) Nest Epiphytes and (*d*) Tank Epiphytes, but this classification once more does not follow quite a proper evolutionary sequence, though these different

classes do form fairly natural ecological groups. The following arrangement follows a slightly more natural order from the standpoint of ecological evolution.

1. The so-called "pseudo-epiphytes" connect very closely with the lianes. They begin their life as climbers and later on become epiphytic by their stems dying off from below upwards.

2. On the other hand, various species of *Ficus*, *Clusia*, *Carludovica*, *Philodendron*, *Anthurium*, etc., reverse this process. At first they are epiphytic, but later they send absorbing roots down into the soil, and they may become independent. When such epiphytes become established in the soil they are practically lianes. Only some of them ultimately kill their supporting host, and remain entirely independent, and of these the banyan figs are the most important, indeed several of them are among the largest, if not the very largest, of all plants. This class is Schimper's "Hemi-epiphytes." They again show the close connection with the climbing habit, but they represent a more advanced type than the pseudo-epiphytes.

3. Proto-epiphytes are forms which obtain their water and food supply from the surface of the supporting structure. They are often xerophytic, often have provision for water storage, as in the pseudobulbs of the epiphytic orchids, sometimes their roots do not differ from terrestrial forms, in other cases they possess velamen. This class includes the majority of the not too highly specialised epiphytes, and it is important to note that many of them occur on rocks or other similar situations where competition from other plants is not too severe or they can be cultivated in soil.

4. Nest Epiphytes. These collect soil and humus in various ways by means of interwoven roots or by "pocket leaves."

5. Tank Epiphytes. These have roots developed only as anchoring organs, or their roots are entirely suppressed so that nutrition is supplied only by the leaves. The Bromeliaceae are the only representatives of this class. They absorb water by means of the peltate scale-hairs situated on their leaf bases. *Tillandsia usneoides* is the most highly specialised of all. When mature, it consists only of thread-like shoots covered with scale-hairs.

6. A few terrestrial herbs appear to connect with and may have been derived from epiphytes. Among the Bromeliaceae, the terrestrial cultivated pineapple is floristically an advanced type. That velamen is not confined to the aerial roots of epiphytic orchids and aroids but occurs on the roots of many terrestrial species as well, has been shown by the work of Goebel (1922), of Moss (1924) and others (cf. Mrs Arber,

1925, p. 16). Not only is velamen found on the roots of a variety of terrestrial orchids, but in forms like *Crinum longifolium, Crinum powellii, Aspidistra elatior, Clivia nobilis, Agapanthus umbellatus.* Many of these are forest margin types, others spread through grassland areas. We have mentioned the fact that many epiphytes are capable of growing in soil and if in general they have, as a group, been evolved from the lianes it seems natural to suppose that they may have given rise to terrestrial forms and not, as is generally assumed, have originated therefrom.

THE ORIGIN AND GENERAL DIFFERENTIATION OF SUFFRUTICOSE AND HERBACEOUS TYPES

Various references have already been made to the different ways in which suffruticose and herbaceous Angiosperms have originated. We have seen that, while certain families may be entirely or predominantly woody, nearly allied but more advanced families may be herbaceous (e.g. Araliaceae and Umbelliferae, Myrsinaceae and Primulaceae) or certain tribes in well defined families may be relatively primitive and woody, other tribes more advanced and herbaceous (e.g. Ehretioideae and Cordioideae as compared with the Borraginoideae among the Borraginaceae). We have seen also that the herbaceous habit may arise within very narrow circles of affinity as in certain large genera, e.g. *Hibiscus, Solanum, Euphorbia.* Burtt-Davy (1922) has dealt with examples of intermediate suffruticose forms arising in several distinct woody genera, e.g. *Acacia, Eugenia, Elephantorhiza, Parinarium, Erythrina, Menodora, Clerodendron* and *Zizyphus.* The work of Jeffrey and Sinnott and Bailey already quoted gives much comparative anatomical information regarding the course of the changes involved. To enter into a discussion regarding their separate viewpoints, and the differences between them, would take us too far (but see Jeffrey, 1917, Jeffrey and Torrey, 1921, Sinnott and Bailey, 1914, 1922). They agree that the herbaceous type among Angiosperms is derivative, a view which Sinnott and Bailey state was apparently first put forward by Hallier (1905).

It is now desirable to examine the possible lines along which the modern herbaceous forms may have been produced. Under the influence of the biota in moist tropical regions one line of evolution apparently has been from trees to woody lianes, then to herbaceous lianes, then to straggling types and finally to herbs. Another possible line has been from trees to lianes as before, then to epiphytes

and then to herbs. But we cannot suppose that these two methods of origin exhaust the possibilities. The mass of evidence from phylogeny brought together in previous articles would appear to indicate that by continued reduction in size, trees gave rise to shrubs, then to undershrubs and these in turn to herbs. There are a multitude of intermediate suffruticose forms which are woody underground or at the base and bear herbaceous aerial branches, but, as already mentioned, these may arise within single large and predominantly woody genera. In the direct passage from tree to shrub, undershrub and herb, however, as a rule the inorganic factors of the environment have played a part—probably a more important part than the biota. Large groups of Angiospermous herbs probably owe their origin to the lowering of temperatures, others to increasing aridity. The numerous and highly differentiated types of herb found in drier and colder regions will be dealt with later. At present we shall confine our attention to the relatively primitive types occurring as undergrowth in the forest as forest margin plants, and as marsh and streambank plants (helophytes). All these habitat types have much in common. They are, to a large extent, independent of climatic differentiation, though, of course, climate does have some effect in controlling their distribution and in the course of time it has also led to some degree of differentiation among them. It should also be remembered that the habitat is of an ancient primitive unchanging type and the great lapse of time has led to differentiation.

Forest Undergrowth, Forest Margin, Marsh and Streambank Types

From the physiological standpoint the most important factors influencing this group are summed up in the term "hygrophilous." The supply of water to their roots is, as a rule, sufficient for all their needs. They may occasionally have to withstand periods of relatively adverse conditions and, just as the dominant trees in tropical forest, because of their inefficiency in water conduction may suffer during brief intervals of drought and, therefore, show some xerophytic characters, such as leathery leaves, so also, many helophytes, particularly in colder and drier regions, may be somewhat xerophytic or, as many writers prefer to express it, "xeromorphic." The xerophytic appearance of many sedges and rushes, etc., has been variously explained as due to "physiological drought," to lack of aëration in the substratum, to accumulation of acids in bogs and swamps and generally by supposing that the process of absorption, even when the

water supply is plentiful, may be interfered with. It is well to remember, however, that in the subtropical regions with dry seasons the water supply, even in marshy places and around forest margins, is not always plentiful. There are intervals of more or less unfavourable conditions. In cold temperate regions absorption is drastically interfered with by the lowering of temperatures in winter when the water may be frozen. It is under such conditions of occasional adversity that xeromorphic helophytes occur. If they are found under conditions that are continually and uniformly favourable, they must be very rare. They hardly occur, for instance, as forest undergrowth in moist tropical regions. If there are exceptions to this rule it should be remembered that their previous phylogenetic history must be taken into account. The epiphytes of tropical rain-forest, as we have seen, usually are more or less xerophytic.

Lack of aëration in the substratum is, of course, often a factor of importance. Correlated with it is the prevalent high development of the intercellular aëration system in helophytes. The substratum is often unstable and plants with underground creeping rhizomes are then predominant. Apart from this, however, owing to the prevailing uniformity of conditions, provision for underground storage is not particularly prominent. Only in colder and drier regions are true geophytes abundant. The creeping underground rhizomes of marsh and forest margin plants bear adventitious roots which help to fix the plants firmly and the plants themselves in turn help to fix the soil. Where growth is continuous food is only stored temporarily and new leaves are continuously produced. This creeping habit of growth is quite unlike the erect habit of woody trees and shrubs but, as we have seen, it is not far removed from the creeping habits of many prostrate forms closely allied to lianes. The light factor is important chiefly among the forest undergrowth types, which connect fairly closely with the more light-demanding forest margin and marsh forms. Probably most shade-loving plants are to be considered rather highly evolved. As a rule they show floristic advance as compared with the more light-demanding types, though some that connect, perhaps directly, with climbing types are more primitive, e.g. among the Araceae.

Systematic Composition and Differentiation

It is impossible to mention all the orders or families which contain plants belonging to this class but the following are the most important: Pandanales, Helobieae, Palmae, Araceae, Gramineae, Cyperaceae,

Eriocaulaceae, Restionaceae, Juncaceae, Commelinaceae, Scitamineae, Orchidaceae, Piperaceae, Ranunculaceae, Rosaceae, Leguminosae, Euphorbiaceae, Malvaceae, Geraniaceae, Begoniaceae, Melastomaceae, Lythraceae, Onagraceae, Halorrhagaceae, Umbelliferae, Labiatae, Scrophulariaceae, Acanthaceae, Gentianaceae, Boraginaceae, Rubiaceae, Valerianaceae, Dipsaceae, Compositae.

The most striking fact is the abundance and dominance of the Monocotyledons. Many of the Dicotyledons are weak stragglers, others are small creeping forms, and there are many suffruticose forms. There are, of course, also many woody shrubs along the forest margins but these have been dealt with already. The woody types become more prominent as the succession advances, and the derivative herbaceous types are ousted, the stages of succession, as already explained, more or less reversing the order of evolutionary development.

The Monocotyledons of this class demand closer attention from the evolutionary standpoint. In all parts of the world to-day where moist situations are not dominated by woody Dicotyledons, they are by Monocotyledons, usually either by grasses or sedges. Theories regarding the actual origin of the Monocotyledons are still too uncertain to allow of much reliance being placed on them, but for those who follow Engler's system of arrangement it is interesting to find that the relatively primitive families more or less all belong to this class, whether we consider the group as a whole or special circles of affinity. In the first case, the Typhaceae, Sparganiaceae, Pandanaceae, Helobieae, many Palms and most of the Araceae are all hygrophilous (or aquatic) or forest margin forms, while in the second case the Eriocaulaceae among the Farinosae and Juncaceae among the Liliiflorae are of the same class.

Both the Pandanaceae and Araceae are particularly interesting since they include climbing forms (and the latter epiphytes as well).

Several of the primitive hygrophilous Monocotyledons are woody, but whether this is significant or not is rather uncertain. The general appearance and form of the arborescent species of *Pandanus* (screw pine) with relatively thin stems supported by stilt roots is similar to dicotyledonous rain-forest woody plants, though the internal organisation is so different. The palms, though many modern representatives are xerophytic, probably had, like the screw pines, an hygrophilous origin. They occur as undergrowth in tropical rain-forest and some of them, e.g. *Nipa fruticans*, are dominant swamp plants lining the landward side of mangrove areas. Other examples

are *Bactris* sp., *Elaeis guineensis* and *Phoenix paludosa*. There are also woody forms among the great dominating families Juncaceae (*Prionium*), Cyperaceae (*Schoenodendron*) and Gramineae (*Bambuseae*). The fact that the bamboos are floristically primitive is interesting, but since the woody habit among Monocotyledons is built up on such distinct lines from the Dicotyledons, in itself it is not generally regarded as necessarily primitive. The woody habit also occurs in types like *Dracaena*, *Yucca* and *Aloe*, which show advanced responses to dry conditions.

We have already noted the fact that the forest margin and marsh types tend to become very widespread. This is largely due to the uniformity and ancient unchanging character of the habitat, though, doubtless, in the actual dispersal of the species the birds that feed in marshy places and along stream banks have played an important part. The ancient tropical forms tend to give rise to isolated species which spread far into temperate regions. This is well seen in the Araceae, where so many evolutionary stages are illustrated. Not only are climbing forms and epiphytes, as well as herbs of the undergrowth, prominent in tropical forest but many marsh forms are widespread in the warmer regions, while types like *Calla* and *Acorus* occur in north temperate regions reaching even to the subarctic zone.

The differentiation of such a typically marsh family as the Cyperaceae is also worthy of detailed and careful study. The separate tribes are, on the whole, sufficiently well-defined. In the tribe Scirpeae the large genus *Cyperus* and its allies are relatively primitive, and are dominant in the tropical regions. More reduced or modified derivative genera like *Heleocharis* and *Scirpus* have spread widely outside the tropics, while the cotton-grass *Eriophorum* is a north temperate or arctic genus. The smaller tribes, Hypolytreae, Rhynchosporeae, Hoppieae and Sclerieae, are, for the most part, found in the warmer parts of the world, and, since they include forms which have the remnants of a perianth, they are, in at least some respects, fairly primitive floristically. Schönland (1922) finds that the general liliaceous floral diagram is fully realised in the South African genera, *Macrochaetum* and *Tetraria*, which have a mountainous south-western distribution—a region where so many very ancient warm temperate types are found, as explained in previous chapters. In the relatively advanced tribe, the Cariceae, the primitive genus *Schoenoxiphium*, which appears to be near the ancestral form of the genus *Carex*, is another African species occurring often around forest margins as well as in marshy places. The huge genus *Carex*, on the other hand,

with about 800 species, has spread all over the temperate, alpine and arctic regions of the world. More intensive work is admittedly required, but so far as a superficial examination permits us to judge, it would appear that all through this great family the evidence from phylogeny lends strong support to the views which we have set forth regarding the origin, differentiation and spread of the hygrophilous herbaceous form. The beginnings are seen under favourable conditions around forest margins, spread takes place through marshes and along stream banks, early responses to temperate conditions are shown on the mountain ranges of the tropics, and particularly on the very ancient mountain ranges of Africa, and the colder temperate regions are occupied by the most highly modified types such as the genus *Carex*.

As was pointed out very briefly in our systematic account the Eriocaulaceae and Restionaceae and allied families, taken together, show exactly the same general course of differentiation. While their origins can be traced back to the forest margins and marshes of the tropics early response to temperate conditions (as in the case of the Restionaceae) are shown on mountain ranges in the south-western region of South Africa and in Australia.

The Juncaceae are important as representing primitive members of the Liliiflorae, considered by some to be allied to the palms. They are hygrophilous but not markedly geophytic. While tropical forms are common enough, and the solitary woody genus *Prionium* is subtropical, on the whole the Juncaceae are mountainous or temperate and, as is to be expected from this distribution, show several features of relative advance. Their xeromorphism has already been discussed. It is only fair to add that all authorities are not agreed that they are to be considered the most primitive members of the Liliiflorae.

The general evolutionary advances reached by this class of derivative plant forms may now best be summarised by giving their main characteristics, structural features and behaviour as follows:

1. The dominant species are nearly always Monocotyledons (grasses, sedges, Restionaceae, Juncaceae, *Typha*, etc.).

2. The majority are perennials, but where a very pronounced dry season leads to a drying up of the water in the substratum, annual species are present.

3. The majority have mesophytic leaves yet some are xeromorphic. The latter, however, are more or less confined to regions where dry or cold seasons occur.

4. Underground creeping rhizomes with adventitious roots fix

the dominant plants firmly in the shifting soil and cause dense social growth producing pure associes.

5. Tufted forms also occur. The tufts tend to be gradually lifted up on their own dead remains and become spongy masses, which lift the water by capillarity—a relatively advanced type of plant form seen for the most part in temperate regions, e.g. *Eriophorum*, *Carex* spp.

6. Among the Monocotyledons the aerial stems are usually unbranched and end in inflorescences.

7. The Dicotyledons are more sparsely scattered, very seldom dominant and are usually weak stemmed, erect or often straggling or creeping forms.

8. When there is a lack of good aëration in the substratum, helophytic species have usually a well-developed aëration system.

PARASITES, SAPROPHYTES AND INSECTIVOROUS PLANTS

The general morphology of these specialised types is very fully dealt with in systematic works, and the larger general text-books of botany, so they may be considered very briefly here. In tropical forest parasites belong for the most part to specialised small families, e.g. Loranthaceae, Balanophoraceae, Rafflesiaceae, and are often very highly modified forms. Hemiparasites on roots are more abundant outside forest areas, in drier, more open types of plant formation or in temperate regions. Their general systematic relationships have already been dealt with. Genera and even species of parasites in many cases tend to become extraordinarily widespread, a fact which is, in some ways rather surprising, considering their highly specialised mode of life and obviously derivative character. It may perhaps be correlated with their possessing, as a rule, very light seeds which are easily scattered by the wind, though wind dispersal in the case of other plants does not necessarily lead to very wide distribution. Saprophytes occurring in tropical forest include the Triuridaceae, Burmanniaceae and many Orchids, as well as other genera such as *Voyria* among the Gentianaceae. Outside the forest areas there are members of the Scrophulariaceae and other families. The problem of saprophytism, and particularly hemisaprophytism, is, of course, intimately bound up with the question of the symbiotic union of flowering plants and mycorrhizal fungi.

The insectivorous plants represent another highly specialised type, but they have been sufficiently dealt with in our general systematic survey.

AQUATIC PLANTS

Hydrophytes or aquatic plants among the Angiosperms are probably all rightly regarded as derivative, though they have originated in many widely separated circles of affinity. Among the Dicotyledons the Nymphaeaceae, Ceratophyllaceae, Podostemonaceae, Hydrostachyaceae, Tristichaceae, Callitrichaceae, and Hippuridaceae are entirely aquatic. Aquatic representatives also occur in many other families, e.g. Ranunculaceae, Cruciferae, Droseraceae, Crassulaceae, Portulacaceae, Elatinaceae, Polygonaceae, Lythraceae, Onagraceae, Umbelliferae, Primulaceae, Gentianaceae, Scrophulariaceae, Lentibulariaceae, Plantaginaceae, Rubiaceae, Compositae. The Monocotyledons include a much higher proportion of aquatics. The whole series of families belonging to the Helobieae are, with very few exceptions, entirely aquatic, as are the Lemnaceae and Pontederiaceae, while water-plants also occur among the Cyperaceae, Gramineae and Sparganiaceae.

The physiology and structure of aquatics are well known and need not be discussed in great detail. Water is a denser medium than air and gases reach the submerged aquatics only through solution. Light is diminished in amount with increasing depth. Most of the structural modifications are to be correlated with these simple facts. In fixed rooting aquatics the roots may absorb water or may act only as fixing organs. Water is also absorbed all over the surface of the plant. The epidermis is thin and usually without cuticle. The occurrence of chlorophyll in the epidermis is to be correlated with the diminished light supply. The water-conducting system is reduced in amount and centrally placed. Secondary growth in thickness rarely takes place, there being, as a rule, no functional cambium. Mechanical tissue is rarely present to any extent. The aëration system is always well developed.

Yet, in spite of the fact that water is a wonderfully uniform environment, and the reactions and modifications mentioned are fairly general amongst all aquatics, the really striking thing about the group is the large amount of differentiation shown. This is, of course, to a large extent understandable in view of their exceedingly diverse points of origin. Much may be explained by taking into account previous phylogenetic history. But in considering the differences between the separate species of the larger aquatic genera, and in considering the differentiation of the well-defined and wholly aquatic families, such as the Podostemonaceae, it is not so easy to

understand how the high degree of differentiation has been brought about. The same problem on a much larger scale is presented by the evolution of life in the sea. It is true that many aquatic species appear to be physiologically sensitive to very slight changes in the external medium, and show corresponding structural changes in leaf size, leaf shape, etc., and it may be the case that the water environment is not so very uniform after all, yet when all possible allowance has been made for the influence of external factors, one is forced to the conclusion that, in the case of the aquatics, internal forces are responsible for a large amount of differentiation, and these internal forces are not much modified in their effects or results by any action of the external environment.

The same thing applies, as we have seen, to differentiation under relatively uniform conditions among land plants as in tropical rain-forest and indeed under all other conditions. The internal forces supply the diverse forms on which the external forces act by sorting out forms suited to each habitat. When the external environment, as in the case of water, is a very uniform one and there is not much competition for space (i.e. when the biota is not important) the diverse forms may, under such circumstances, very well persist. The biota, however, in the case of aquatic plants, is often of at least some importance as it is to a much greater extent in tropical rain-forest.

The General Evolutionary History of Aquatic Forms

Aquatics have not all become equally highly specialised. There are all gradations between forms, which do not differ markedly from land plants and such very highly modified types as the Lemnaceae. The classification of aquatic plants adopted by Mrs Arber in her recent work (1920) follows an earlier scheme of Schenck and essentially it represents a rough evolutionary sequence.

1. Plants rooted in the soil.
   - A. Essentially terrestrial forms that can live in water without marked adaptation (*Achillea ptarmica, Cuscuta alba, Glechoma hederacea*).
   - B. Essentially terrestrial forms which sometimes produce modified submerged leaves (*Sium latifolium*).
   - C. Plants which produce three types of leaves, submerged, floating and aerial (various Helobieae, *Ranunculus*, etc.).
   - D. Submerged plants with aerial foliage leaves or aerial inflorescences.
   - E. Entirely submerged plants with hydrophilous pollination.

F. The highly modified, commonly thalloid, Podostemonaceae, Hydrostachyaceae and Tristichaceae.

2. Non-rooted Aquatics.

A. Floating.

B. Entirely or partially submerged.

This scheme of classification represents one of the earliest attempts to arrange any class of plant forms in an evolutionary sequence. Aquatics among flowering plants, as a rule, represent a final and specialised evolutionary stage. Once the aquatic habit has been definitely adopted, as it appears to have been in many cases early in the history of the Angiosperms (especially the Monocotyledons), a subsequent return to land life among forms resulting from further differentiation has rarely taken place.

According to a theory of Scott's (1890), however, the origin of polystely in Dicotyledons is due to such infrequent occurrences. Aquatic plants, as we have mentioned, have generally no functional cambium. A structure once lost, according to Dollo's "Law of Irreversibility," which has been further elaborated for plants by Mrs Arber (1920, p. 181 and p. 336), cannot be regained. If any aquatic returns to terrestrial life it has difficulty in renewing its cambium. Instead of doing so, according to Scott, it meets the increased demand for a vascular-carrying system by multiplying the number of steles. *Gunnera*, *Auricula* and *Pinguicula* are examples of terrestrial plants which may have had aquatic ancestors.

If it be admitted, as it is by most botanists, that the aquatic plant form is derivative, then it must be granted that the above scheme of classification is a perfectly natural one, proceeding as it does from the purely terrestrial to the most completely aquatic types. It is interesting, therefore, to note that, as in the case of the xerosere so also in the hydrosere, the successive evolutionary stages are the reverse of the stages of the plant succession. The usual stages of the plant succession in the hydrosere everywhere are (1) Floating aquatics, (2) Rooting submerged aquatics, (3) Reed grasses, *Typha*, etc., with only their lower parts submerged, (4) Sedges and other marsh plants, (5) Hydrophilous shrubs or herbs, (6) Mesophytic vegetation. The plant succession proceeds from the aquatic to the mesophytic and terrestrial. The evolutionary differentiation of the plants concerned has proceeded in exactly the opposite direction. So that generally both for the stages of the xerosere and the hydrosere, plants appearing relatively early in the plant succession are relatively highly evolved ecologically.

SUMMARY

1. Under moist favourable conditions the effects of the biota are of paramount importance, resulting in the production of various derivative types of plant form, lianes, epiphytes and terrestrial hygrophilous suffrutices and herbs. The latter occur as forest undergrowth and forest margin types but tend to spread widely in marshy situations and along stream and river banks. The specialised types of parasites, saprophytes, insectivorous plants and aquatics are also considered.

2. Lianes belong to a large number of diverse families and in their evolutionary history progress from the woody to the herbaceous and from the hygrophilous or mesophytic towards the xerophytic. Woody scrambles which sometimes grow erect, woody lianes of fixed climbing habit, half-woody or herbaceous lianes with organs often modified for climbing, herbaceous geophytic lianes, xerophytic lianes, annual lianes and creeping herbaceous stragglers, which do not grow erect, are different classes arranged somewhat roughly in an evolutionary sequence.

3. Epiphytes connect with lianes the so-called "pseudo-epiphytes" or climbing forms which become epiphytic, forming an intermediate group. Hemi-epiphytes reverse this process. Proto-epiphytes are the class including the orchids, aroids, etc., where the epiphytism is definitely fixed. Nest epiphytes and tank epiphytes are still more specialised. There are a few indications from phylogeny as well as from comparative morphology (the occurrence of velamen on the roots of terrestrial herbs) that epiphytic forms may have sometimes become terrestrial.

4. Herbs of the forest margin, marshes and stream bank may have originated often from climbers or epiphytes, but the herbaceous form in general, with increasing climatic differentiation probably arose frequently by reduction in size of woody plants giving a series, trees, shrubs, undershrubs and herbs. The series is illustrated even with the limits of many large genera. In this class of herbaceous forms the dominant species are usually monocotyledonous, perennial plants with underground rhizomes. The Dicotyledons are usually weak-stemmed, erect or straggling species. Tufted forms also occur. In regions with adverse seasons xeromorphic or annual forms are found.

5. The specialised classes of parasitic saprophytes and insectivorous plants, since they are well known in their general features, are dealt with very briefly.

6. Aquatic plants are classified according to the scheme (originally due to Schenck) adopted by Mrs Arber in her recent book. Progressive stages are shown from land forms to the most highly modified of floating aquatics. The evolutionary series more or less reverses the stages of the (hydrosere) plant succession.

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CHAPTER VI

THE EFFECT OF CLIMATIC DIFFERENTIATION ON DERIVATIVE TYPES

WE have seen how, under the influence of the biota, during long-continued favourable conditions, various derivative types of plant form have been produced. The effect of drier and colder conditions have been referred to continuously throughout, but it is now necessary to consider in greater detail the effects of the process of climatic differentiation on the non-woody forms. Schimper's classification of vegetation into three types, woodland, grassland and desert, is fundamental. Of these, woodland, according to our view, is relatively primitive, grassland and desert both derivative. The analysis of vegetation has, of course, proceeded very far since Schimper's time. Schimper regarded woodland and grassland as antagonistic types. "Woodland and grassland stand opposed to one another like two equally powerful but hostile nations, which in the course of time have repeatedly fought against one another for the dominion over the soil." A clearer understanding of plant successions, however, has shown that, while grassland in forest climatic areas may form a stage in the plant succession and ultimately be ousted by forest, yet in other areas it represents a climax stage. A grassland stage in the plant succession to forest may be a necessary stage as much as the youth of an individual is necessary before adult development can be reached. To speak of warfare between stages of the plant succession is unnecessary and misleading. In various plant successions stages succeed one another usually more or less as follows: (*a*) Open colonising stages consisting of ruderal, often annual, species, and xerophytic forms; (*b*) Xerophytic deep-rooted grasses; (*c*) Mesophytic grasses; (*d*) shrubs; (*e*) Low-growing, much-branched, light-demanding trees; (*f*) Tall trees able to endure shade in their juvenile stages.

Now in the relatively favourable climatic areas the full succession may be shown. In less favourable areas the succession may stop at any of the stages, down to the first opening stage in desert regions. As already mentioned, the separate stages are roughly the reverse of the order of evolutionary development of plant forms. We have

already dealt with the climax and subclimax stages dominated by woody plants which are the most primitive.

We must now deal with the earlier stages, and since grassland types play such an important part it is necessary to consider in some detail the evolutionary history of the grasses themselves.

The Floristic Differentiation of the Grasses

That the Gramineae are allied to the Cyperaceae appears to be without doubt, though it is possible that the two families may have been developed from ancestral forms (possibly forms like the Juncaceae) along parallel lines. The sedges, on the whole, have not progressed so far as the grasses, and are still more or less confined to primitive types of habitat. The views of various writers on the history of the Glumiflorae as a group do not help us much. Wettstein (1898) derives them from the Helobieae, through the Liliiflorae, with other groups such as the Scitamineae representing parallel or diverging lines of development. Schumann (1904) points out their similarity in vegetative characters to the Zingiberaceae among the Scitamineae. Lotsy (1911) derives the two families separately from a group like the Juncaceae among the Liliiflorae. Metz and his co-workers (1924), on serological grounds, look on the Glumiflorae as derived from the advanced Liliiflorae close to the point of origin of the Scitamineae. Sargent and Arber (1915) have carried out extensive work on their seedling anatomy which tends to confirm their origin from the Liliiflorae. We need not pursue this uncertain subject further. All the views that have been held would favour an origin for the grasses in hygrophilous warm habitats.

Hackel's work in Engler and Prantl's *Pflanzenfamilien* still remains the basis of all modern systems of classifying the grasses. The Gramineae, however, from the systematic standpoint are a difficult group. The limits of the tribes are none too well defined, and their inter-relationships are rather uncertain. The order of arrangement of the tribes adopted by Hackel is certainly not a phylogenetic one. It may be doubted whether the separation of the tribes into two series—the first with the spikelets reduced and falling from the rachis entire, and the second with the spikelets often many flowered and with the rachilla articulated above the empty glumes—is by any means a natural subdivision.

In any case it is the second series which contains the most primitive forms, since reduction in the number of flowers in the spikelet has almost certainly been one of the main evolutionary

trends. While the reduction is universal among the tribes included in Hackel's Series I it occurs also fairly commonly in Series II. It is a process which has taken place like so many general evolutionary trends, within many narrow circles of affinity. Hackel places the bamboos at the end of his second series, yet clearly the bamboos are floristically primitive.

Though it is easy to criticise Hackel's arrangement, and it has been modified in detail by Stapf and others, yet when any attempt is made to initiate any drastic changes in the grouping of the genera the difficulties are very great.

The tribes themselves are probably as natural as they can conveniently be made. We shall content ourselves, therefore, with an examination of some of the evolutionary trends within them and a few remarks on their probable ecological interrelationships and differentiation.

The Bambuseae are a very distinct tribe with woody, rarely herbaceous culms, and with the leaf-blade often with a short slender petiole, articulated with the sheath, from which it finally separates. Their flowers come nearest to the ordinary monocotyledonous type. There are usually three large perianth segments (or lodicules) which are very seldom wanting. The stamens are often six in number, sometimes more. In some genera the filaments are united in a tube. There are often three styles. The fruit in the Dendrocalameae and Melocanneae is a nut or berry instead of a caryopsis.

The bamboos are distributed somewhat unevenly throughout the tropical zone. Generally they are found outside of or surrounding the rain-forest areas. The monsoon region of Asia is particularly rich in species, but they are common in tropical America and less common in Africa. They have penetrated into subtropical regions and even into temperate regions. All through the tropics they tend to produce mountain types. In the Himalayas they ascend to an altitude of over 10,000 feet and still higher in the Andes. In Ecuador *Chusquea aristata* reaches the snow line. In their ecological differentiation some are tree forms, and they may occur, not in clumps, but isolated, e.g. *Melocanna bambusoides*, a tall tree which has a fleshy apple-like fruit 8–12 cm. in diameter and seeds the size of betel nuts. The majority have short underground rhizomes which send up numerous culms forming clumps. Some species are climbers, e.g. species of *Arthrostylidium*, *Arthroostachys*, *Merostachys*, *Chusquea*, *Bambusa*. Finally there are a number of herbaceous forms, e.g. *Puelia* and *Atractocarpa* in Africa and *Planotia* in South America

(on the elevated plains of Colombia). *Planotia* is described by Hackel as having long narrow panicles, with small numerous spikelets, of the same structure as those of the nearly allied *Chusquea*, and the habit of the Festuceae, with herbaceous, almost leafless culms and leaves crowded together close to the ground. The leaves are usually continuous, not articulate, with the sheath. *P. nobilis* has the largest leaves of any grass (1·5–4·5 m. long by 8·30 cm. broad). It is important to note further that several of the climbers (*Arthroostachys, Microstachys* and *Chusquea*) as well as the herbaceous *Planotia* show floristic advance in having the stamens reduced to three, the fruit a true caryopsis and the spikelets one-flowered.

Though the Bambuseae, therefore, are in many ways somewhat isolated, yet the gap between them and the Festuceae is not so very great. Herbaceous members like *Planotia* help to bridge it over, and it is very interesting again to find that the transition from the tropical types to temperate takes place on mountain ranges.

Apart from its possible connections with the primitive Bam buseae, the tribe Festuceae in its widest sense as defined by Hackel has chief claims to be considered the most primitive of the ordinary grasses, though even within this tribe certain conspicuous evolutionary advances have been made. In the subtribe Arundineae the genera *Phragmites* and *Arundo*, or forms very like them, go back to the Cretaceous. *Arundo* has many-flowered spikelets, almost woody stems, and broad flat leaves. These tall-growing hygrophilous types are generally distributed through the warmer regions of the world, recalling the bamboos in many of their features, but the common reed grass (*Phragmites communis*) is cosmopolitan. Reactions to drier conditions within the tribe are seen in the genera *Ampelodesmos* of the Mediterranean region and in *Gynerium*, the Pampas grass of South America. The subtribe Centotheceae have their leaves broad and net-veined, and include half a dozen small genera from various parts of tropical Africa, Asia and America (in the case of *Lophatherium* reaching Japan). In the Eu-Festuceae the large genera *Poa* and *Festuca* are well represented on the mountain regions of the tropics, and have played an important part in establishing the dominance of the meadow grass or sod-forming type in cold temperate regions. The same subtribe shows advances in other genera, especially in the adoption of the annual habit, e.g. in such genera as *Schismus, Sclerochloa, Wagenheimia* and *Lamarckia* as well as in species of *Briza, Brizopyrum, Poa*, etc., in various xerophytic types, e.g. *Lasiochloa*, or halophytic types, e.g. *Aeluropus* and *Atropis*.

The other subtribes must be passed over with the briefest possible reference. The Pappophoreae are mostly tropical, but include many forms which have reached to dry conditions, e.g. *Pappophorum, Schmidtia, Triraphis.* The Sesleriae similarly include creeping grasses of the seacoast (*Monanthochloë*), low grasses of elevated plains (*Munroa*), annual steppe or desert grasses (*Ammochloa, Urochlaena*), xerophytic forms (*Fingerhuthia*) and alpine grasses (*Sesleria, Oreochloa*). The Eragrosteae and Triodieae include several genera important in drier subtropical and temperate grasslands, *Triodia, Diplachne, Molinia, Eragrostis, Koeleria.* The Meliceae have a few small genera: *Ectrosia* and *Heterachne* in Australia, *Harpachne* in tropical Africa, *Anthochloa* in the Andes, *Diarrhena* in Japan and North America, and the large genus *Melica* throughout the temperate zones and mountains of the tropics except Australia.

The Brachypodieae (*Bromus, Brachypodium*) are also temperate or mountainous in distribution.

In brief, the Festuceae in general show primitive connections with hygrophilous tropical vegetation in the Arundineae and other forms, but as a whole have become highly differentiated first of all probably on mountain ranges of the tropics and subtropics but later to suit most of the highly diverse modern climatic habitats, both in drier subtropical areas and in temperate regions.

The tribe Aveneae, like the Festuceae, have some claims to being considered primitive, indeed the two tribes Aveneae and Festuceae might be grouped together. From their study of the anatomy of embryos and seedlings Sargent and Arber (1915) place *Avena* as nearest to their hypothetical ancestral form, but the number of forms dealt with were not very many and further work is needed. Within the tribe there is a general tendency to reduce the number of flowers in the spikelet to two, and one genus, *Holcus*, of temperate and mountainous distribution, has the spikelets readily deciduous as a whole, as in the tribes belonging to the first series of Hackel. Several of the genera of the Aveneae are temperate or mountainous, South African or Australian, e.g. *Danthonia, Pentaschistis, Achneria.* These genera in South Africa mix with the sclerophyllous shrubs, and are abundant without ever assuming dominance. The warm temperate flora of Africa and Australia, we have already noted, has many ancient characteristics. As we have seen, the flora of the Mediterranean shows many connections and here again the Aveneae are represented by special genera, e.g. *Antinoria, Molineria, Airopsis,* while the larger genera are more widespread, e.g. *Aira, Deschampsia,*

Trisetum, Avenastrum, Arrhenatherum extending into the cold temperate regions and, like the heathers, some of them being especially characteristic of moorland areas. Not only in the dominant evergreen shrubs, therefore, but also in the associated grasses the connections between the ancient mountain flora of Africa, the flora of the Mediterranean region and the moorland flora of cold temperate Europe are well marked. The Aveneae also include a few tropical or subtropical genera, e.g. *Coelachne, Tristachya, Trichopteryx,* adapted to dry grassland conditions, and numerous annual species of *Avena* in the temperate regions.

Other tribes of the second series are all probably more advanced than the Festuceae and Aveneae. The Hordeae have the spikelets arranged in an equilateral spike, and the genera are all somewhat specialised, including many annual or ruderal perennial forms, e.g. species of *Lolium, Triticum, Hordeum, Agropyrum,* sand-dune species, e.g. *Elymus arenarius.* The subtribe Nardeae includes only one species, *Nardus stricta,* which has the spikelets one-flowered, the spikes unilateral, and only one stigma, being in many ways the most advanced type of all. Its distribution in Europe and northern Asia is, therefore, again very interesting from our present standpoint.

The Chlorideae have one-sided spikes or racemes and include important prairie grasses of North America (e.g. *Bouteloua, Buchloë*), seashore types (e.g. *Dactyloctenium, Spartina*), important creeping surface-rooting types (e.g. *Cynodon*), ruderal grasses (e.g. *Chloris, Eleusine*), xerophytic or mountain forms (*Microchloa, Harpechloa, Tripogon, Tetrachne*).

The Agrostideae have the spikelets regularly one-flowered and include the subtribes Stipeae, Phleoideae and Euagrosteae. Of these the Euagrosteae are the least specialised, and include the large genus *Agrostis* with over a hundred species distributed over the entire globe, but most frequent as meadow grasses in the northern hemisphere. *Ammophila arundinacea,* a sand-dune species, also belongs here.

The genus *Sporobolus* with over 80 species includes prairie grasses, ruderal grasses, xerophytic subtropical grasses and one widespread halophyte, *S. pungens.* The Phleoideae have a number of Mediterranean genera (*Cornucopiae, Crypsis, Heleochloa, Maillea*), a dwarf Arctic polar grass (*Phippsia*), and the larger temperate genera *Alopecurus* and *Phleum.* The Stipeae include some forest grasses (e.g. *Milium effusum, Stipa dregeana*) but in general the great genus *Stipa* with over 100 species is adapted to grassland

conditions. *Stipa pennata, S. tirsa* and *S. capillata* are the most important grasses of the Russian steppes. The genus *Stipa* is also prominent in the North American prairies. *S. tenacissima* is the esparto grass of Spain and North Africa. The genus *Aristida* is equally important, containing about the same number of species. *Aristida* is the most important genus of xerophytic grasses in the early stages of the plant succession in most regions of subtropical grasslands and (in the section *Stipagrostis*) in all the semi-desert and desert regions of Africa and western Asia. In view of what has already been said regarding the general course of evolutionary differentiation and its relationship to the plant succession it is particularly interesting to find that both *Stipa* and *Aristida*, with their single-flowered spikelets and other advanced characters, represent about the highest stages of development in all these tribes so far dealt with.

The Phalarideae are not so advanced. Though the spikelets are one-flowered they have two extra empty glumes or male flowers below the terminal one and the number of stamens is variable (two, three, four or six). In many respects indeed they are a tribe, which seems to have retained certain primitive features and they are often mountainous in their distribution, e.g. *Ehrharta* in South Africa which connects with *Microlaena* and *Tetrarrhena* in Australia. The genera *Anthoxanthum* and *Hierochloë* extend from the mountains of the tropics to the temperate or frigid zones. Stapf has removed the tribe Oryzeae from the first series of Hackel and has placed it near the Phalarideae. Sometimes in the Oryzeae there are numerous empty glumes and six stamens. The genera are mostly tropical and hygrophilous but *Leersia oryzoides* occurs in north temperate swamps, and *Lygeum spartum* on the high plains of countries bordering the Mediterranean. Both the Oryzeae and the Phalarideae have no close connections with the other tribes.

Hackel's first series consists of tribes which are, on the whole, clearly distinct from those of the second series. Though, floristically, they show a high degree of specialisation yet in some respects they have retained primitive characters. They have not become widespread in the cold temperate regions, but, on the other hand, they are the most abundant grasses of the moist tropical regions. It would seem that, long after the earlier hygrophilous and mountain types among the bamboos and Festuceae had begun to give rise, by differentiation, to types which were well adapted to colder conditions, and drier conditions, forms were evolved which became dominant in subtropical grassland areas. What the exact origin

of the latter has been it is difficult to say. The two main tribes are the Andropogoneae and the Paniceae. The Andropogoneae include some hygrophilous forms, especially in the subtribe Sacchareae, but the majority are of the "bunch grass" type, dominant in mesophytic or somewhat xerophytic tropical and subtropical savannahs and extending into temperate regions. The genus *Andropogon* as defined by Hackel is a very large one now subdivided by Stapf. The grass *Themeda triandra* is dominant over immense areas of grassland in Africa. The Paniceae include hygrophilous genera, e.g. *Setaria* and *Pennisetum*, shade-loving forest forms, e.g. numerous species of *Panicum*, creeping surface-rooting forms, e.g. *Stenotaphrum*, many ruderals, e.g. species of *Panicum*, *Paspalum*, etc. The Paniceae are not so prominent in tropical and subtropical grassland areas. Like some rather highly evolved tropical herbaceous families among the Dicotyledons, e.g. the Acanthaceae, they are most in evidence around forest margins and in hygrophilous situations, playing an entirely subordinate rôle in the vegetation, or they occur as tropical weeds. The tribe Maydeae are a still more specialised small group of tropical or subtropical forms which include the cultivated *Zea mays* and do not call for any special analysis.

Though there are many very primitive grasses in the tropics (as the Bamboos, Arundineae and other Festuceae) the dominant grasses of the subtropical regions are clearly of a rather highly evolved and probably recent phylogenetic type, much more so than the temperate forms. This is quite parallel to what we have learned concerning the evolutionary history of woody types. While the moist, tropical forest areas contain the most ancient types of all, the drier subtropical areas contain many very recent forms, including succulents, etc. The reactions to increasing aridity and especially to desert conditions have apparently taken place at a much later stage than the reactions to cooler or temperate conditions.

Ecological Differentiation among the Grasses

As in the separate families of trees and shrubs so among each of the different tribes of the Gramineae differentiation has proceeded rather far. Even within the limits of a single genus widely different forms have been produced. It is difficult to arrange the different forms in any exact evolutionary series, though, as we have seen, the evidence from phylogeny as regards the characters of the spikelet support the view that, in general, xerophytic types, and types which appear early in the plant succession, ruderal and annual

forms, etc., are all highly evolved (e.g. *Aristida, Stipa, Cynodon, Sporobolus, Spartina,* etc.). The following classes of forms are ecologically more or less distinct and they represent the final result at the present day of the process of differentiation in this important group but it is not easy to say what the relationships between the different classes have been.

1. Woody types. The Bamboos.
2. The Reed type. Tall-growing forest margin and marsh forms of which the Arundineae are primitive examples, but the same form is adopted by some advanced types among the Paniceae, etc., e.g. *Pennisetum purpureum,* the elephant grass of Africa, and others.
3. Tufted hygrophilous forms with short underground rhizomes. They differ from the Bamboos and Reed Grasses in being much smaller forms.
4. Mesophytic Bunch Grasses (Andropogoneae, etc.).
5. Xerophytic Bunch Grasses (*Aristida,* etc.), a highly evolved type floristically and otherwise. [This ends one line of evolutionary advance.]
6. Sod forming grasses with extravaginal stolons or runners most abundant in temperate regions. Phylogenetically rather primitive forms.
7. Creeping, surface-rooting, and psammophilous forms with long rhizomes. A generally rather heterogeneous class, which have apparently arisen at several different levels of evolutionary development.
8. Climbing grasses and shade-loving scrambling forest species, hygrophilous forest margin stragglers. A few of these are undoubtedly ancient, as among the Bamboos, but the majority are rather highly evolved floristically. The Paniceae include a large number.
9. Annual grasses. These are to be regarded as modern forms but they have arisen, as in the case of the annual plants, in many widely separated circles of affinity in the different tribes.

The General Distribution of Grasses and Grasslands

In all the tropical and subtropical areas with increasing aridity forest passes into open "savannah forest" and then into savannah proper, which consists of grassland with scattered trees or patches of forest. Finally there are great areas of grassland without trees. The Campos of Brazil are savannah with low-growing trees isolated like the trees in a grassy orchard. The Llanos of Venezuela are pure

grassland with trees, few in number and more or less confined to moister spots. The Pampas of the Argentine are immense areas of more or less pure grassland.

In Africa exactly the same stages are represented—equatorial forest, grassland with forest in the moister areas, open "tree-veld" (savannah) of every possible degree of increasing xerophytism and, once more, great stretches of pure grassland (grassveld). From the north-eastern forest areas of Australia inland towards the dry interior and towards the south, similar gradations are shown.

Over all the great areas of tropical and subtropical grassland the stages of the succession are similar. Pioneer deep-rooted wiry grasses form the early stages, while bunch grasses of a more mesophytic character become dominant in the climax stages. Much of the tropical grassland occurs in forest climatic areas where the true forest stages have been destroyed by fire. The grassy Patanas of Ceylon, the Lalang vegetation of south-eastern Asia, with *Imperata arundinacea* dominant, the elephant grass areas of central Africa with *Pennisetum purpureum*, possibly much of the African grassveld, much of the South American llanos and campos and possibly also some of the eastern prairies of North America are due to a retardation of the natural forest succession or the destruction of climax stages.

The grasslands of temperate regions also cover very large areas in North America, Europe and Asia. In North America, according to Shantz (1924), they may be divided into (1) tall grass (prairie), grassland with bunch grasses (*Andropogon* spp.) and sod grasses (*Stipa* and *Agropyrum*, etc.) nearest the eastern side and most mesophytic, but also occurring on the Pacific side. (2) Short grass (plains), grassland with grama grass (*Bouteloua*), buffalo grass (*Bulbilis*), wire grass (*Aristida*) and also *Agropyrum*, *Stipa*, *Koeleria*, etc., a drier type occurring west of the 100th meridian and east of the Rockies. (3) Mesquite (desert) grassland with other species of *Bouteloua*, *Hilaria*, *Scleropogon* and *Aristida*, the driest type of all occurring in Texas, New Mexico, Arizona and Mexico.

The steppe regions of Asia and Europe form a vast belt between the northern forests and the central deserts. In many parts the (chernozem) soils are remarkably fertile. The steppe grasses are mostly of the tufted type, species of *Stipa* being dominant with *Koeleria cristata*, *Festuca ovina*, etc. The genus *Stipa* is also most prominent in all the drier steppes, such as occur in Hungary (the pusztas), Roumania and Serbia, and in Spain (the Iberian steppes).

The meadows of temperate countries occur in regions where the precipitation is fairly high and evenly distributed; often no doubt they replace former forests. Meadow grasses belong to the genera *Poa, Festuca, Agrostis, Aira, Avena, Dactylis, Holcus, Anthoxanthum, Alopecurus, Phleum, Briza* and others. Many are sod-formers, e.g. *Poa pratensis, Festuca rubra, Agrostis* spp., etc., yet, on the whole, the tufted forms are even more numerous as regards species. The grasses are all mesophytic.

In mountain regions natural meadows occur in many parts of Europe, Asia and America of different types, either wet or dry. Alpine meadows of the Rockies, for instance, have *Carex* spp. and *Festuca brachyphylla* dominant with a great variety of alpine plants. Some authors would include the eastern prairies as meadow.

Vast though those regions of subtropical and temperate grassland are, they by no means contain all the grasses. As already pointed out in the regions of sclerophyllous vegetation grasses are very numerous though rarely dominant. They are chiefly rather primitive forms, at least floristically, including members of the Festuceae, Aveneae and Hordeae.

The great genus *Danthonia* and its allies are prominent at the Cape and in Australia, while related genera, e.g. *Aira* and *Deschampsia* and *Molinia*, are characteristic of moorland regions in Europe. *Nardus stricta* is a highly evolved northern member of the Hordeae.

The grass-heath or grass-moor type of north temperate grassland has *Nardus stricta, Molinia caerulea, Deschampsia flexuosa* and *D. caespitosa* with *Agrostis* spp. and *Anthoxanthum odoratum*, etc.

In Britain the "silicious grasslands" (Tansley, 1911), which often replace woodland, have *Nardus* and *Deschampsia flexuosa, Agrostis tenuis*, with *Molinia*, the last named in wetter places.

Another class of grass forms which do not, as a rule, enter into the composition of grassland areas are the psammophilous types occurring on sand dunes and along the seashore. A few seashore grasses are true halophytes, growing in salt or brackish water; the psammophilous creeping forms, which root at the nodes, are efficient sand-binders. Many of this class tend to be very widespread, e.g. *Spartina stricta, Sporobolus pungens*, etc. The seashore habitat, like the hygrophilous, is relatively uniform all over the world.

We also have to take into account all the other types of grasses which play a subordinate rôle in vegetation, viz. the climbing forms in forest (e.g. species of *Panicum, Olyra latifolia, Stipa dregeana, Potamophila prehensilis*), the hygrophilous marsh species, some

primitive like the Arundineae, others highly developed, the ruderal perennial creeping forms and the annual types. The subordinate grasses of all kinds are undoubtedly mixed in their origin. From the nature of things the earliest grasses must have been subordinate and many ancient forms remain so but the class of subordinate forms, as a whole, has been added to throughout the evolutionary history of the grasses. While a considerable amount of our limited space has been devoted to the question of the origin and differentiation of the grasses and the establishment of grasslands, the importance of this section of our subject clearly justifies it. Nothing else has had a greater influence on the general course of evolutionary history among flowering plants, as well as among the higher animals, than the fact that so much of the total surface of the globe has become completely dominated by this very successful type of plant. It will be necessary now, however, to consider the differentiation of other derivative types of plant form more briefly.

The General Differentiation of Derivative Types in Response to Cooler and Drier Conditions

Since Raunkiaer's system of classifying the lifeforms of plants is now well known, it is convenient, as far as possible, to refer to his names for the different classes. His classes of Chamaephytes, Hemicryptophytes, Geophytes and Therophytes, arranged in this order (omitting helophytes and hydrophytes) show successive increased responses to adverse conditions and, therefore, to some extent, illustrate an evolutionary sequence. But it should be clearly realised that one class has not necessarily produced the next, though the different classes do grade into one another. Moreover, since the biota has been chiefly concerned in their production we have removed many forest margin Chamaephytes or Cryptophytes and have associated them with Helophytes as representing a primitive class of forms which have not been forced to react to any extent to climatic differentiation.

On the other hand, it cannot be maintained that the Chamaephytes of drier areas have all been derived from forest margin hygrophilous forms. As we have seen, many woody genera of trees and shrubs have by reduction of size, given rise to species which are chamaephytic, geophytic, or even therophytic.

Raunkiaer's class of Nanophanerophytes pass by insensible gradations into the class of Chamaephytes. It may be doubted whether Raunkiaer's "normal spectrum" has been as accurately

computed as he believed, though that is a minor point. He assigns only 1 per cent. of the world's flora to the two classes of Hydrophytes and Helophytes combined, which would give a total of about 1440—a figure that seems much too low.

Without applying Raunkiaer's names too rigidly we shall follow his sequence and, where possible, subdivide his classes into certain fairly well defined forms, as follows:

1. Prostrate Chamaephytes. These are either suffruticose or entirely herbaceous. Through the hygrophilous types this class may connect with the straggling lianes. Evolutionary advance here, as elsewhere, has gone hand in hand with increasing xerophytism.

2. Cushion forms. These forms represent a final result of the tendency towards increased branching combined with decrease in size. The cushion-type is sometimes very dense and compact, being rounded or hemispherical in outline. Plants of this type occur in desert or semi-desert regions, in alpine situations and in cold countries. They are commonest at high altitudes on mountain ranges all over the world. One of the most extreme examples is the well-known *Raoulia* (mountain sheep) of New Zealand. Hauri (1912), in a full discussion of the morphology and ecology of cushion plants, distinguishes between (1) typical cushion plants consisting of a single individual with compact texture, (2) cushion-like dwarf shrubs which are less compact and (3) cushions formed of several distinct plants of the same or different species.

3. Herbaceous succulents. The physiological significance of the succulent habit has already been discussed in connection with trees and shrubs, but there are altogether relatively few woody succulents. The vast majority are herbaceous or, at most, suffruticose. Such smaller forms are completely dominant over great stretches of the South African Karroo and they are common in similar dry regions elsewhere. The fact that they are, as a rule, highly evolved floristically is very striking, especially such forms as *Mesembryanthemum*, *Euphorbia*, the Stapelieae, etc. Halophytes are also generally more or less succulent and include many rather specialised herbaceous forms in different circles of affinity. Other succulents are found in rocky places, in waste places as ruderals, and in various open situations.

Other well-defined forms occur among the Hemicryptophytes and intermediate types.

4. Rosette (or half-rosette) plants. This type is brought about by a shortening of the internodes and a consequent crowding of

the leaves. In addition to increased protection various other advantages are supposed to accrue, e.g. the obtaining of heat from the soil and the utilising of dew deposited at night. Rosette forms are common in a great variety of situations showing all gradations from the mesophytic to the xerophytic. They occur in hygrophilous marsh and forest margin situations throughout the grassland areas, in waste places and open situations of all kinds and in semi-desert and desert regions. On the whole they are commoner at high altitudes than at lower and Bonnier showed that some species, which at low altitudes have long internodes, produce rosette forms in alpine situations. The rosette form is often combined with succulence and often also with the next class.

5. Plants with woody "rootstocks." This is a very common type in grassland areas. The aerial parts are herbaceous or very slightly woody and die back each year (or they frequently are burned off) leaving an underground woody stem or "xylopodium" as it has been called by Lindman (1900). The renewal buds are just below the soil surface, as a rule, but they are very irregularly placed, and the general form of the aerial growth of branches varies considerably. Sometimes it is tufted or caespitose, sometimes straggling or, if the underground rhizome itself tends to spread, the class becomes transitional to the travelling geophytes which, however, are further distinguished by their rhizomes and renewal buds being more deeply buried in the soil. This class in the other direction, as already explained, connect fairly obviously with the phanerophytes.

6. Travelling geophytes. These have horizontally placed underground rhizomes, which give rise either to aerial foliage leaves or to erect epigeal shoots which bear leaves. As we have seen, they are common among the forms occurring around forest margins and in marshy situations and are, therefore, to be reckoned rather primitive in their origins. They may even connect with the lianes, epiphytes and stragglers of the forest undergrowth. In a word the biota has been largely concerned in their production apart altogether from increasing climatic differentiation, a fact which illustrates once more how Raunkiaer's system tends to fail as a phylogenetic system of classifying lifeforms. Travelling geophytes also are common as psammophytes on sand dunes and as perennial weeds in cultivated land.

7. Mat-geophytes. These are the so-called bulbous plants, though the storage organs may be stem tubers (or corms) or root tubers, as well as true bulbs. They are stationary forms, feebly-

branched, and have renewal buds well protected. Though numerous Dicotyledons are geophytic the majority are monocotyledonous, especially the Liliaceae, Amaryllidaceae, Iridaceae and Orchidaceae. Several of the genera in these families are very large and widespread (e.g. *Allium* (300 sp.), *Scilla* (100 sp.), *Ornithogalum* (90 sp.), *Lilium* (50 sp.), *Tulipa* (50 sp.), *Hypoxis* (60 sp.), *Iris* (125 sp.), *Moraea* (60 sp.), *Gladiolus* (150 sp.), *Crocus* (60 sp.)). Raunkiaer's estimate of 3 per cent. of geophytes for the whole world's flora, which would give a total of 4300, is again probably too low. I have estimated the total for Natal as 18 per cent (Bews, 1916). Though geophytes have probably had very ancient origins, much of their differentiation has been relatively recent. They are especially abundant in drier subtropical and temperate grassland areas.

More attention should be given to their physiological behaviour. While in some, probably the more recent types, new storage organs are formed annually, in others the storage organs are perennial and may go on enlarging year after year. In the drier subtropical areas water as well as food material is stored underground by geophytes. Their renewal of growth in spring is then determined largely by rise in temperature rather than by the incidence of the first rains.

In general they flower in spring, often before they renew their foliage, and recommence the work of assimilation. In many cases the formation of tubers is known to be intimately bound up with infection by fungi, and a general fungal theory of tuberisation is favoured by many (see Bernard, 1902, 1909; Coulter, Barnes and Cowles, 1911; Magrou, 1921).

8. Therophytes. Annual plants, though they have been produced in very widely diverse circles of affinity, are to be generally regarded as the most recent of all forms. Under natural conditions they are particularly characteristic of the most adverse regions and situations (deserts and open xerophytic habitats). A high proportion of all desert floras consists of short-lived ephemerals, which spring up after the infrequent rains, pass through their whole vegetative life in the course of a few weeks, flower, form seed and die. The angiospermous seed in its most highly evolved form, with hard resistant seed coats and long viability, is the most efficient organ of all in resisting adverse conditions. Annuals are also peculiarly suited to the types of habitat which have resulted from man's interference and they are abundant as weeds in cultivated land or as ruderals generally in waste places. Many such types have become very widespread as a result of man's activities.

The physiological processes of annual plants, though most fully investigated and best known, since such plants can be most easily and quickly grown for experimental purposes, are of a somewhat specialised character, like the plants themselves. Annuals do not in their vegetative life react in the same way as perennials. They do not store food except in their seeds and until they begin seed production their growth follows Blackman's *Law of Compound Interest* (1919). They are thoroughly efficient assimilating machines, they expand their total leaf area as much as possible so as ultimately to produce seed as efficiently as possible, but their whole life-cycle differs from perennial forms where storage takes place in vegetative organs. Biennials are related to annuals. During their first season, most biennials develop a rosette of leaves and store up food. In their second season an erect shoot is formed which bears flowers and forms seeds. The biennials are characteristic of cold temperate countries.

Habitat Forms

While the life-forms of plants always bear a certain definite relationship to the habitats where they occur, yet the origin of the different forms has been due, partly at least, to internal forces which are entirely independent of the environment. Views still differ as to the exact relationship of the internal and external forces influencing evolutionary differentiation. Some believe that the environment does nothing more than sort out the material supplied through the agency of the independent forces, which result in variations great or small. Others are more inclined to think that the external environment may not only use the material already supplied, by selecting the types best suited to its varying requirements, but may exercise a guiding influence over its actual production, that it may lead directly to permanent changes in the basic hereditary developmental processes, and not merely deal with the results of processes over which it has no controlling influence. The recent work of Harrison and Garrett (1926) on the induction of Melanism in the Lepidoptera, and its subsequent inheritance supplies definite proof that environmental influence can be brought to bear, powerful enough to influence the germ plasm of animals. As far as plants are concerned botanists have always been more inclined than zoologists to adopt the Neo-Lamarckian standpoint.

But in dealing with the facts of distribution and of ecological differentiation in general we have begun at the other end of the scale. We have taken the great main classes of plant forms and have tried

to analyse the history of their phylogenetic differentiation. When we come down to more minute differences, such as are exhibited within the limits of a species, the relationship of our subject to modern ideas in genetics, becomes more obvious. Turesson in various recent papers (1922–5) has endeavoured to show that the mass of genetically different biotypes, which make up the Linnean species do not distribute themselves indiscriminately over an area comprising different types of localities. The biotypes, on the contrary, are found in nature to be grouped into different types each confined to a definite habitat. The Linnean species from the standpoint of "genecology" Turesson designates the "ecospecies." The habitat types he terms "ecotypes" and he looks upon them as the products that have arisen through the sorting and controlling effect of the habitat factors upon the heterogeneous species population. The ecotypes are *genotypical* responses of an ecospecies to particular habitats, as Turesson claims to have shown by cultural experiments. One and the same ecospecies thus succeeds in populating widely different habitats. On the other hand, phenotypical reactions may result in the production of reaction types which are due entirely to the modificatory influence of the environmental factors. These are called "ecophenes" by Turesson. Whether this distinction between ecophenes and ecotypes is quite so definite and necessary as Turesson believes or may not be due merely to a lack of fixation in the former, there can be no doubt that the numerous facts recorded for the different species dealt with are extremely valuable. In his latest paper Turesson has shown that a differentiation of parallel ecotypes takes place within different species, a fact which makes a uniform system of naming possible. The following ecotypic names are proposed: oecotypus *campestris*, oect. *arenarius*, oect. *salinus*, oect. *sub-alpinus*, oect. *alpinus* and numerous ecotypes of different species investigated are placed in their respective groups. While Turesson's names are very convenient as applied to habitat forms within the Linnean species (ecotypes of the ecospecies) the term "habitat form" has been applied in a wider sense to the distinct species which have reacted in definite ways to distinctive habitats.

Thus Warming has distinguished the main classes, hydrophytes, mesophytes, halophytes, xerophytes, as well as (in his later work) helophytes, oxylophytes, psychrophytes, psammophytes, chersophytes, psilophytes, lithophytes and eremophytes. In such a classification of plant forms the "life-form" concept is, to a large extent, abandoned, and emphasis is laid wholly on the habitat. It follows

from what has been shown in all the preceding chapters that, in a very general way, some of these habitat forms are more ancient than others. Xerophytism is a general evolutionary trend and xerophytes are, as a rule, derivative, as are hydrophytes in another direction. The ancient unchanging types of habitat, it may be repeated, are more likely to contain ancient forms than modern types of habitat. But it has also been shown that previous writers have not laid sufficient emphasis on the effects of the biota. There are hosts of derivative types even among the mesophytic or hygrophilous plants of tropical rain-forest, i.e. among those that occupy subordinate positions in that ancient plant community.

It may be well, however, in conclusion, to examine very briefly a few habitat forms (using the term in the wider sense), which have not been sufficiently dealt with already.

1. Halophytes. Saline soils occur near the seashore, near salt springs and salt lakes and in dry steppe or desert regions. The halophytic flora is, on the whole, a poor one, but various families have a few or many halophytic genera or species, e.g. Chenopodiaceae, Tamaricaceae, Frankeniaceae, Aizoaceae, Plumbaginaceae, Portulacaceae, Zygophyllaceae, Cruciferae, Helobieae, Cyperaceae, Gramineae, etc. The prevalent succulence of halophytes is largely a direct response to the salinity of the habitat since halophytes commonly lose much of their succulence when grown in soils poor in sodium chloride. Other of their characters are more definitely fixed. Along the seashore many halophytes are very widespread, e.g. *Ipomaea pes-caprae*, species of *Canavalia*, *Salicornia*, *Suaeda*, *Atriplex*, *Sporobolus*, *Spartina*, *Triglochin*, etc. Inland, in salt pans, salt deserts, etc., species of *Suaeda*, *Salicornia*, *Salsola*, *Frankenia*, *Tamarix*, *Statice* are most characteristic and widespread.

2. Psammophytes. The soil in this case is immature and usually sterile and all the vegetation more or less xerophytic. Long creeping rhizomes or very deep roots are the characteristic feature of psammophytes. With advance in the plant succession shrubs and then trees take possession and the sand becomes definitely fixed with resulting changes in the soil conditions. In Europe, dune heath with *Empetrum*, *Calluna*, etc., or dune bushland with *Hippophaë*, etc., or finally pine forest, as on the Baltic coasts, represent successive stages. Similarly in the sclerophyllous regions Macchia is the climax stage, in North America poplars, willows, or coniferous forest, in Asia species of *Pinus*, *Betula*, *Populus*, *Salix* and *Ulmus*. In tropical and subtropical regions psammophilous scrub or forest include a

variety of species, in which the family Sapotaceae (*Mimusops, Sideroxylon,* etc.) are often rather prominent or in wetter types, *Barringtonia racemosa, Hibiscus tiliaceus,* etc., are very widespread. In Brazil the littoral forest on sandy soil is known as "restinga."

3. Psychrophytes, or plants of very cold habitats, are a still more heterogeneous group occurring in subglacial areas on high mountains or in the circumpolar regions. They are dwarf shrubs, suffrutices or herbs. Nanism is the prevailing characteristic in all the species, both in the plants as a whole and in their separate organs. Leaves are small, internodes short, or if the shoots are elongated then they are prostrate. Cushion plants, rosette forms and tufted forms are common. Ethereal oils, anthocyan pigments, etc., are sometimes a feature.

4. Other habitat forms of Warming may be passed over with very brief reference. Lithophytes proper (rock surface plants) consist mostly of lower forms of plant life. Chomophytes (Chasmophytes) or rock crevice plants have few special characteristics and usually include samples of any plants occurring in the neighbourhood. The Chersophytes or plants of waste land are highly evolved, often annual types, but they have already been sufficiently dealt with, as have also the Mesophytes, sclerophyllous plants and Psilophytes (grassland plants). Warming's class of Oxylophytes (plants of sour soils) is the least satisfactory of all these habitat forms. Their general distribution and physiognomy probably depend on climate, and the sourness of the soil is a *result* of the combined effects of climate and vegetation and is not the *cause* of responses. We have already discussed the connections of moorland plants and the more ancient mountain sclerophyllous types.

5. The Tundra vegetation Warming includes among his moorland oxylophytic types. It covers great areas in the northern parts of Europe, Asia and America. The soil is wet and the air moist but the low temperature checks absorption. The landscape is monotonous, desolate and treeless. Two types are distinguished, the moss-tundra and the lichen-tundra—the former moist, the latter dry. The moss-tundra consists of mosses with dwarf shrubs including *Empetrum, Betula nana* and *Vaccinium myrtillus* and small herbs with often brilliantly coloured flowers, which in places are rather abundant. In the lichen-tundra, a thick carpet of fruticose lichens (*Cladonia,* etc.) gives the landscape a characteristic yellow-grey colour. Between the lichens are found *Empetrum, Betula nana, Loiseluria procumbens, Calluna, Juniperus communis* and other dwarf shrubs, *Nardus*

stricta, Deschampsia flexuosa and herbs, e.g. *Hieracium* spp. The tundra vegetation obviously connects with the moorland and through that with sclerophyllous vegetation. Its chief interest is that it represents the most impoverished and most extreme type of response to cold conditions.

6. Desert plants. Warming includes both desert and steppe plants in his eremophytes, though steppe plants in general should rather be classed with psilophytes even though the drier types of steppe do grade into deserts. It is true that the term "desert" is used rather vaguely by different authors so as to include any fairly dry region, e.g. the South African Karroo and other "shrub steppes." The best test of real desert conditions from the vegetation standpoint is a very high proportion of annuals. In true desert the individual perennials are few and far apart. They are universally of the most extreme class of xerophytes, usually either succulent or thorny or often both. The annuals often tend to cluster round the scattered bushes of perennials so that even in desert there is a kind of plant succession, which, however, is the reverse of the usual order. Desert plants represent the final result of specialisation in response to increased aridity.

SUMMARY

1. Among all the responses shown by Angiosperms to climatic differentiation in many ways the most important has been the evolution of the grasses—a type which has been successful in assuming complete dominance over vast areas of the world's surface. An attempt has, therefore, been made to analyse the floristic and ecological differentiation of the grasses in some detail.

The bamboos are regarded as the most primitive and they are tropical in distribution, but have produced some herbaceous forms on the mountains of South America, which suggest a possible origin for the Festuceae and Aveneae, tribes which, on floristic grounds, are regarded as the most primitive of the ordinary grasses. The subtribe Arundineae remain mostly hygrophilous and tropical. Even within the limits of the Festuceae, however, forms have been evolved to suit most modern climatic conditions. The same applies to the Aveneae and Hordeae. Connections are shown in all these tribes between the mountain types of the southern hemisphere and tropics and the Mediterranean region and moorland grasses of the northern hemisphere. The Chlorideae are a more advanced tribe and the Agrostideae have reached a high evolutionary level in the subtribe Stipeae which include *Stipa* and *Aristida*, the former the chief type

in steppe regions and the latter in drier subtropical regions. The Phalarideae and Oryzeae are not apparently closely connected with other tribes, and in some respects have retained primitive characters, but again show specialisation in various directions. The tropical and subtropical grasses belong mostly to the tribes Andropogoneae and Paniceae, the former being dominant over large areas of subtropical grassland, the latter more subordinate types around forest margins in moist places and as weeds. All these tropical and subtropical grasses are rather highly evolved as are most derivative types of woody plants in the drier tropical and subtropical regions.

2. Ecologically the grasses have become differentiated to give (1) woody types, (2) the reed type (both rather primitive), (3) tufted hygrophilous forms, (4) mesophytic bunch grasses, (5) xerophytic bunch grasses (along one line of response), (6) sod-forming grasses, (7) creeping, surface-rooting and psammophilous forms, (8) climbing grasses and shade-loving scramblers, (9) annual grasses. The last mentioned are probably usually recent types but the interconnections between the other forms are rather uncertain. In each tribe and in much narrower circles of affinity, even within the limits of the larger genera, a variety of very distinct forms commonly occur.

3. An account of the general distribution of the grasses and grasslands of the world is given but it can hardly be condensed any further in this summary.

4. In classifying other derivative types which have responded to drier and cooler conditions Raunkiaer's sequence of arrangement is followed, but it is modified somewhat since the different classes of derivative plant form have had diverse points of origin. The following fairly well defined types are described: (1) Prostrate chamaephytes, (2) Cushion forms, (3) Herbaceous succulents, (4) Rosette plants, (5) Plants with woody rootstocks, (6) Travelling geophytes, (7) Mat-geophytes, (8) Therophytes.

5. In connection with "habitat forms" Turesson's recent work is discussed with reference to the differentiation of the Linnean species (ecospecies) into various habitat forms (or ecotypes). In a wider sense classes of "habitat forms" have been recognised by Warming and others made up of different species which have reacted in a similar way. Most of these, e.g. xerophytes, mesophytes, helophytes, hydrophytes, etc., have been sufficiently described in earlier chapters but a few notes are added on halophytes, psammophytes, psychrophytes, tundra vegetation and desert plants.

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